

CHAPTER IV
ATLANTIC SPOTTED DOLPHIN VOCALIZATIONS

Signal exchange is an important requirement for sociality and social cohesion (Bekoff, 1977; Herman & Tavolga, 1980; Smith, 1986). The sounds of free-ranging cetaceans, and specifically odontocetes, have been recorded and described for several species, including bottlenose dolphins (Caldwell & Caldwell, 1965; Tyack 1976; Caldwell *et al.*, 1990), sperm whales (*Physeter macrocephalus*, Watkins *et al.*, 1985; Weilgart & Whitehead, 1993), pilot whales (*Globicephala melas*, Weilgart & Whitehead, 1990), humpback whales (*Megaptera novaeangliae*, Payne & McVay, 1971; Payne *et al.*, 1984; Silber, 1986) and right whales (Clark, 1983). Several studies have investigated the variety of sounds, and their potential social functions and significance, produced by whales and dolphins. Vocal behavior has been correlated with various activities and contexts in dolphins and whales, including but not limited to, feeding (e.g., D'Vincent *et al.*, 1985; Norris *et al.*, 1985), social cohesion (e.g., Norris *et al.*, 1985; Ford & Fisher, 1986; Silber, 1986; Tyack 1986a), and resting and traveling (e.g., Norris *et al.*, 1985; Sjare & Smith, 1986). Clark (1983) observed that sounds of southern right whales (*Eubalaena australis*) were significantly correlated to the activity, size, and sexual composition of whale groups. Simple and predictable sound structures were associated with greater distances between individuals; while complex and variable calls were more strongly associated with socially interactive groups. Humpback whales produce both songs and social sounds that vary according to gender and activity: that is, only males produce songs while on the mating grounds (Tyack, 1981). With playback experiments, it was determined that humpback whales respond to feeding calls and group social sounds (Tyack, 1983; Mobley *et al.*, 1988).

Toothed whales are much smaller on average in size (except for sperm, killer, and bottlenose whales), and generally found in larger groups with less distance among individuals than for baleen whales. Early studies on free-ranging dolphin sounds tended to focus on rate and general vocal type produced. Sjare and Smith (1986) documented a general association between beluga whale (*Delphinapterus leucas*) surface-behavioral activity and types

of vocalizations. The authors categorized vocalizations into three broad types: whistles, pulsed calls (including clicks and pulsed tones), and noisy vocalizations. They defined behavioral activities that included resting, directed swimming, socially interactive, and alarmed. Weilgart and Whitehead (1990) conducted similar observations on pilot whales in Newfoundland waters and determined that the complexity in vocalizations was positively correlated with more complex interactions in behavioral activity among individuals and within the group. They suggested that pilot whale vocalizations served to maintain contact and coordinate movements of the group.

Most of the studies on the vocal behavior of wild dolphins focused on sounds as related to the surface activity of the animals in question because of the difficulties associated with identifying and following a single individual vocally, especially in choppy and murky sea conditions. Work on captive dolphins has indicated that dolphins are proficient at vocal mimicry (Tyack, 1986b; Richards *et al.*, 1984, Reiss & McCowan 1993); are able to understand syntax and label objects with sound (Herman *et al.*, 1984, 1993, 1994); and possess the ability to learn vocalizations (Tyack, 1986b; Sayigh *et al.*, 1990; McCowan & Reiss 1995c). In the captive environment, it is often possible to identify which of several animals is producing sound because individual dolphins can be physically and acoustically identified. Devices such as dataloggers and voca-lights, developed by Tyack (1985), can be attached to a dolphin's melon via suction cups. These instruments facilitate the identification of a whistling individual in captive groups of two to three animals.

Early investigations into the functions of free-ranging dolphin vocalizations, especially whistles, were hindered because researchers were unable to identify the vocalizing individuals (Tyack, 1976; Sjare & Smith, 1986; Weilgart & Whitehead, 1990). While it is generally true that cetaceans do not exhibit concurrent external signs with their vocalizations, as can be observed in many terrestrial animals through posturing or movements associated with vocalizing (e.g., Goodall, 1986); occasionally, dolphins do emit a stream of bubbles when vocalizing (e.g., Caldwell & Caldwell, 1972; Pryor, 1990; Dudzinski, pers. observ. 1992-1995). The level of coincidence between whistle emissions and bubble streams is not known, although recent work by

McCowan and Reiss (1995a, c) suggests that bubbles are often produced by infant dolphins when whistling. Bubble emissions may be an accidental artifact of vocalizing, may be a function of age or excitement level, or may be associated with other internal referents (Gewalt, 1979; Smith, 1986; Pryor, 1990). For example, bubbles have been documented to be used by humpback whales during feeding in Alaska (D'Vincent *et al.*, 1985; Sharpe & Dill, 1993) and also during agonistic interactions in the Hawaiian waters (Silber, 1986). Silber (1986) suggested that male humpbacks use bubbles to obscure themselves from conspecifics and to displace competitors from position near a female.

DELPHINID VOCALIZATIONS

Delphinid vocalizations have been broadly partitioned into three categories: frequency-modulated tones, often referred to as whistles; clicks; and burst-pulsed sounds (Herman & Tavolga, 1980; Tyack, 1986a, 1986b; Au, 1993). From captive animal work, high-frequency clicks, ranging from 120 to 140 kHz, have been correlated with sonar or echolocation functions in dolphins (Au, 1993). Because of the highly directional nature of these echolocation clicks, direct evidence of their use in the wild is difficult to gather. Burst-pulsed sounds have been qualitatively described in several delphinids, for example Hawaiian spinners (*Stenella longirostris*, Norris *et al.*, 1985; Östman, 1994), bottlenose dolphins (Caldwell *et al.*, 1965; Tyack, 1976; Herman & Tavolga, 1980), common dolphins (*Delphinus delphis*, Caldwell & Caldwell, 1968), orca (*Orcinus orca*, Bain, 1986; Ford & Fisher, 1986), and pilot whales (Weilgart & Whitehead, 1990). Since burst-pulsed sounds have a broad-band frequency range (with highest energy often above human hearing and conventional recording capabilities), are usually short in duration, and vary in intensity, they do not present parameters that are readily measured and compared within and among species. Thus, burst-pulse sounds are not analytically well-represented or discussed in the literature. In contrast, whistle sounds, which are tonal and frequency-modulated (FM), have been studied extensively in captive and wild bottlenose dolphins (e.g., Caldwell & Caldwell, 1965; Tyack, 1976; Herman & Tavolga, 1980; Caldwell *et al.*, 1990; Wang, 1993). Whistles are FM on a range from 3.0 - 24.0 kHz on average, depending on the species. They have a relatively narrow frequency

bandwidth; that is, on the scale of a single, short spectral estimate, energy is concentrated in a narrow frequency band. Whistles generally vary from 0.5 to 2.5 s in duration, but again whistle length can vary considerably with species and individual.

Context-specific vocalizations were described and discussed for captive dolphins in the late 1960's and early 1970's (e.g., Dreher and Evans, 1964; Evans, 1967; Kaznadzei *et al.*, 1976). Focusing primarily on whistles, they reported a large repertoire within social groups, sharing of whistles across social groups, and a predominant but not individualized whistle type. Dreher and Evans (1964) suggested that dolphin vocalizations varied more according to situation or activity than by individual. In contrast, Caldwell and Caldwell (1965) provided the first evidence for the production of signature whistles in dolphins. They defined signature whistles as individually distinctive according to the contour pattern on the spectrogram (frequency versus time plot of the sound); and, that these whistle contours comprised the majority (74 - 90%) of an individual's whistle repertoire (Caldwell & Caldwell, 1965; Caldwell *et al.*, 1990). Smolker *et al.* (1993) and Sayigh (1992) discuss the variability in identified signature whistles. The data of these researchers supported previous work concerning whistle variability: while differences in certain aspects of the spectrogram display were apparent (e.g., duration, frequency shifts), the shape of the whistle contour pattern remained relatively constant. Caldwell *et al.* (1990) proposed that the signature whistle was an identity broadcaster used to inform conspecifics of an individual's presence (hence, the origin of the signature whistle hypothesis (SWH)).

Most early work investigating signature whistles focused on captive dolphins, primarily because of the relative ease of identifying vocal individuals (e.g., Caldwell & Caldwell, 1965, 1972; Caldwell *et al.*, 1973; Tyack, 1986b; Caldwell *et al.*, 1990). Smolker *et al.* (1993) presented evidence for the use of signature whistles during separations and reunions of free-ranging mother/calf pairs of bottlenose dolphins in Shark Bay, Australia. The presence of signature whistles in bottlenose dolphins in Sarasota Bay, Florida, and evidence for the use of individual signatures as identity labels between non-related dolphins in social groupings were documented by Sayigh (1992). Use of signature whistles as contact calls between separated

mother/calf pairs of bottlenose dolphins was also observed by Sayigh *et al.* (1990, 1995) in Sarasota Bay, Florida.

Recently, Janik *et al.* (1994) determined that different aspects of contextual information are present and related to the structural variation in signature whistles (e.g., in start and end frequencies, and signal duration). Thus, information other than identity is available in whistles of dolphins, indicating that individuals may provide information on their behavioral state or other referents when communicating with conspecifics. While Janik's work does not preclude the existence and function of signature whistles, that of McCowan and Reiss (1995a, 1995b) offers the whistle repertoire hypothesis (WRH) as an alternative to the SWH. In their studies of three captive social groups of bottlenose dolphins, individuals produced many different whistle types and also shared several types within and across social groups. McCowan and Reiss (1995b) suggest a less predominant role for signature whistles within the whistle repertoire of an individual dolphin than has been discussed by proponents of the SWH. They further suggest that whistles vary across social contexts among groups.

SPOTTED DOLPHIN VOCALIZATIONS

With the exception of early work by the Caldwells and colleagues (1971, 1973) and a few studies investigating spotted dolphin vocalizations at the population level (Moore, 1990; Wang, 1993), little information has been gathered on the acoustic emissions of Atlantic spotted dolphins. Herzing examined sounds from spotted dolphins in northern Bahamian waters (Herzing & Davis, 1993; Herzing, 1994). She described seven vocalization types including signature whistles, excitement vocalizations, genital buzzes, squawks, screams, barks, and synchronous squawks. Frequency range and duration, behavioral context, and age category were noted for each type of vocalization. However, without spectrograms to exhibit contours, it is difficult to compare the vocalization types, as described by Herzing, with other work on spotted dolphin sounds (e.g., Caldwell *et al.*, 1973; Moore, 1990; and results below).

Caldwell and Caldwell (1966) provided the first description of Atlantic spotted dolphin vocalizations from recordings of two captive individuals. Clicks, chirps, squeals, barks, growls, and signature whistles were

documented and compared with the "more vocal" bottlenose dolphin (Caldwell *et al.*, 1971). Clicks were considered to function in environmental exploration and feeding, while burst-pulse sounds conveyed a "more emotional" intent (Caldwell & Caldwell, 1971). The latter were more frequently associated with social interactions between individuals. Evidence for signature whistles in spotted dolphins was presented by Caldwell *et al.* (1973), although the authors suggested that spotted dolphins have fewer, or less distinct, differences in whistles between individuals than bottlenose dolphins.

OBJECTIVES OF SPOTTED DOLPHIN SOUND ANALYSIS

This section of my dissertation focuses on the sounds produced by Atlantic spotted dolphins. My main objective is to present a description of the various vocal types produced by individuals within the study population. An examination of the production of different vocal types (e.g., whistles, clicks, squawks) as related to behavioral activity, group type and size, and class and gender of vocalizing individuals is provided.

Two factors facilitate the collection of vocal behavior data from specific individual spotted dolphins. First, these dolphins are habituated to the presence of snorkelers and do not appear adversely affected by swimmers (see Chapter II and III). Second, with new methodologies (see Appendix D), I have been able to identify the vocalizing dolphin for approximately 38% of the recorded vocalizations. Investigations into dolphin vocal behavior as related to: dolphin age, gender, and individual identification; the activity of interacting animals; and group composition are thus possible because of the ability to observe individual dolphins in close proximity and to identify the vocalizing dolphin.

I expect vocal types to vary according to behavioral activity and to group composition. It is likely that spotted dolphin vocal activity is related to the activity of interacting group members; for example, dolphins engaged in social activity might produce more varied vocal types as compared to dolphins involved in foraging or travel activities. Conversely, it is possible that vocal behavior is simply a reflection of group size, assuming that groups with more activity have more individuals. I would expect production of vocal types to vary according to dolphin gender and age (spot class). It is possible

to examine the difference in vocal type according to dolphin age and gender separate from group type and size; and therefore, to examine if production of vocal types varies by group composition (type) distinctly from dolphin gender and age.

Looking specifically at spotted dolphin whistles, I expect that whistle contours (represented by the frequency versus time plot on a spectrogram) will vary more by context and behavioral activity (i.e., within individuals) than by individual dolphin (i.e., between individuals). The study population of spotted dolphins is comprised of at least 95 recognizable individuals (see Chapter 2, Appendix A). If whistles varied more by individual, then I would expect to record at least 95 distinct contour patterns from this group. If whistles varied more by behavior and were shared between individual dolphins, then I would expect a much lower number of whistle contours based upon the general categories of behavioral interaction among dolphins.

METHODS

Sounds produced by Atlantic spotted dolphins were recorded during swim encounters with a mobile video/acoustic (MVA) system (see Chapter II; Appendix D). Group type, group size, and behavioral activity of the group were documented for each encounter with spotted dolphins and were independent of the classification of vocalizations from videotapes. When determined, the identification of the vocalizing dolphin, spot class, and gender were also documented. The specific action pattern and any external referents (e.g., sea cucumber, passenger, other dolphins) were described for sounds when the vocalizing dolphin was identified.

For vocalizations recorded when dolphins were not within the camera's field of view, it was not possible to determine the class or gender on the vocalizing individual, or even to identify the sound producer. The same was true for video segments when dolphins were in tight groupings and at least five meters from the MVA system (Appendix D). Thus, the sample sizes for gender and class categories reflect only cases where I was certain of the identity of the vocalizing dolphin. In some cases, the location of the vocalization was determined, but the exact identification of the individual dolphin could not be identified because dolphins were too far from the MVA system or because dolphins were grouped too closely. These cases represent

the differences in the sample sizes between class and gender according to vocalizations.

Recorded sounds were characterized and defined aurally from tapes during the digitizing process (see below) and visually from spectrograms, with attention to the literature for delphinid vocalizations (Wood, 1953; Caldwell & Caldwell, 1971; Caldwell *et al.*, 1973; Herman & Tavalga, 1980; Norris *et al.*, 1985; Moore, 1990; Sayigh, 1992). Following the protocol used in most previous studies on dolphin acoustics, vocalizations were divided into three broad categories: frequency-modulated tones (such as whistles and chirps), clicks or pulsed vocalizations, and burst-pulse vocalizations (such as squawks). A click train was defined as a series of clicks produced by a dolphin.

A recorded sound was classified by its aural characteristics and contour pattern (from a spectrogram) and assigned to a particular vocalization category. Recordings that contained a combination of the sounds from any of the above three categories of vocal types were noted, but each specific sound was analyzed to category whenever possible. Vocalizations that were not immediately able to be classified were labeled onomatopoeically (e.g., screams, squawks, and whines). Further analysis of the spectrogram parameters (see below) facilitated classifying these sounds to type, or established a new type within the three defined vocalization categories. Occurrences of two or more vocal types, produced simultaneously or overlapping in part on their contour patterns from the spectrogram, are termed "joint" vocalizations. Joint vocalizations are classified according to each vocal type present. A descriptive discussion of joint vocalizations is presented in the results.

Bubble emissions produced concomitant with vocalizations were documented (for the variety of bubble emissions, see Appendix C). Vocal behavior was noted on data forms for all encounters; however, only aural impressions of vocal behavior (i.e., vocal types produced) and the relative number of sounds were available for encounters that were not videotaped. Vocal types that were audible to snorkelers during these encounters were noted (e.g., whistle, click train, squawk), with the class, gender, and identification of the vocalizing dolphin documented. These data provided

general information on the level of vocal production as related to behavioral activity, group type, and interactions among individual dolphins.

SOUND RECORDING AND ANALYSIS TECHNIQUES

Vocalizations from, and vocal interactions among, dolphins were recorded onto Hi-8 videotape with a mobile video/acoustic (MVA) system (Dudzinski *et al.*, 1995, Appendix D). This system consisted of an audio stereo Hi-8 video camera (Sony model CCD-FX710) with a level audio recording response to 20 kHz. Two omni-directional hydrophones (each with a level response from 0.14 - 14 kHz and a sensitivity of -162 dB re 1 volt) were cabled through the underwater housing into the camera. Hydrophones were mounted in styrofoam backing to decrease sensitivity to high frequency sounds to the sides and back of the recording system (Dudzinski *et al.*, 1995).

Recording of sounds from individual dolphins and from groups of dolphins was opportunistic, dependent on environmental conditions and dolphin proximity to and around the research vessel and snorkelers. As outlined in Chapter III, once the recording system and handler were in position, and the group type and behavioral activity assessed, a focal dolphin was chosen and followed.

All recorded sounds were digitized at the Bioacoustics Research Program (BRP), Cornell Laboratory of Ornithology, New York. All sounds were digitally acquired from 0 to 24 kHz at a sampling rate of 48 kHz for computer analysis: an internal digital signal processing DARE card coupled with an advanced customized version of the Canary software program was used to sample and store digitized sounds (Charif *et al.*, 1995). Analysis of sounds was performed at BRP and at the Marine Mammal Research Program (MMRP), Texas A&M University at Galveston, Texas. Digital spectrograms were computed using a 256 point FFT, a Hamming window function, 50% overlap, and 256 point frame size. Resulting spectrograms had an effective filter bandwidth of 187.5 Hz, and a grid resolution of 187.5 Hz by 2.67 ms. At BRP, a Quadra 950 Macintosh with a 300 MB hard disk partition, 64 megabytes of RAM, and a 21 inch rasterops display was used to make spectrograms and to perform analysis on recorded and digitized sounds. At MMRP, a Macintosh Powerbook 180, with a 300 MB hard disk, 28 megabytes of RAM, and a 16 bit

gray scale monitor was used to make spectrograms and to conduct analysis on recorded sounds.

Whistles were arbitrarily categorized to contour type based upon the most-frequently observed contour patterns (frequency versus time plot of a whistle) on spectrograms. This generated categories of whistles which may or may not reflect distinctions made by the dolphins. Counting the numbers of different contour types observed from whistles of spotted dolphins provided data to evaluate if these dolphins possess individually distinct, or signature, whistles.

STATISTICAL ANALYSES

Spotted dolphin vocalizations are discussed descriptively according to vocal type. Average frequencies and signal durations are presented for comparison to the vocalizations of other delphinids. Ranges of these measurements are also presented for comparison.

Chi-square statistical analyses were used to compare the occurrence of vocal types according to three variables (Zar, 1984): behavioral activity, group type and spot class of the vocalizing individual. Since the numbers of minutes of observations of each behavioral activity, group type, and spot class were not equal across categories within each variable, expected numbers of occurrences were standardized by the effort of observation. Expected values were calculated by dividing the number of minutes in each category by the total number of minutes across categories with a variable (e.g., behavioral activity), then multiplying the result by the observed number of vocalizations per vocal type. As an example, if the total number of minutes across behavioral activities was 595, the number of minutes in all social contexts was 223, and the number of observed whistles was 934, then the expected number of whistles for social contexts would be 350. That is, $E = (O_i) * (N_c / N)$, where " O_i " is the number of observed vocalizations in a vocal type; " N_c " is the number of minutes in a particular category of the variable; and " N " is the total number of minutes for all categories for a variable. For the example given, this would translate to $(934) \times (223 / 595) = 350$ expected whistles during social activity.

Statistical analyses were made with Microsoft Excel 4.0 (Excel user manual 1990) and Statistica (Statistica for Macintosh, 1994) software packages

on a Macintosh Powerbook 180. Anecdotal and descriptive reports of spotted dolphin vocal and behavioral activity are presented to support statistical manipulations of the data.

RESULTS

A total of 1805 vocalizations were digitized from videotapes for 1993 and 1994 (969 in 1993; 836 in 1994, see Table 13). Frequency-modulated tones, including whistles and chirps, represented a larger number of vocalizations than the click trains or burst-pulse vocalizations. It is possible that click sounds were under-represented within the data because of the more directional nature of dolphin click sounds (Au, 1993). Still, due to equipment limitations in the frequency ranges or recorded sounds, the clicks recorded were below 20 kHz. It is possible that the click trains recorded during this study represent the low-frequency portion of the higher frequency echolocation clicks. Or these clicks could be a low frequency click separate from the echolocation clicks. Further analysis of specific parameters (e.g., the rise time of the beginning portion of a click waveform) of these click trains may present evidence to support either possibility. Concurrent use of equipment (e.g., Nagra recorder, hydrophone sensitive to high frequency) to record the higher frequencies of spotted dolphin vocalizations while using the MVA system could provide evidence as to whether these low frequency click trains are distinct from echolocation clicks or aspects of the latter.

VOCAL TYPES PRODUCED BY THESE SPOTTED DOLPHINS

This group of spotted dolphins produced a variety of sounds both vocally and behaviorally. The latter class of vocalizations included tail slaps and jaw claps. The sounds produced by these behavioral actions are not discussed in detail due to exceptionally low sample sizes ($n=1$, $n=3$, respectively). Data collected in this study focused on vocalizations produced underwater. Vocal types included whistles, chirps, screams, click trains, whines, and squawks. Click trains and whines seemed to differ primarily in repetition rate; they were grouped during analysis when comparing vocal type to behavioral activity, group type, and spot class. These two types of click vocalizations most likely have different functions (see below), but were grouped as click trains since samples of whines were relatively low ($n = 10$ in

1993; 8 in 1994). Whines are discussed qualitatively below with regard to dolphin behavior. All vocal types were recorded in more than one behavioral activity and from at least two different spot classes.

Table 13. Recorded sample sizes of vocal types. Numbers of "joint voc's" are already included in vocal type sums and therefore not added into the total for each year.

<u>VOCAL TYPE</u>	<u>1993</u>	<u>1994</u>	<u>TOTAL</u>
whistles	451	483	934
chirps	216	97	313
screams	19	0	19
click trains & whines	164	200	364
<u>squawks</u>	<u>119</u>	<u>56</u>	<u>175</u>
TOTAL	969	836	1805
<u>joint voc's</u>	<u>217</u>	<u>163</u>	<u>380</u>

Frequency-modulated Vocal Types

Whistles recorded from spotted dolphins during this study varied in duration from 0.5 s to 2.5 s and ranged in frequency from 5.6 to 19.2 kHz (see examples in Fig. 16). These frequency-modulated tones often had greater than one inflection point (defined as a change in the direction of the slope of the contour pattern on a spectrogram, e.g., negative going to positive). This change in inflection was termed a "loop" by the Caldwells in the late 1960's. Spotted dolphin whistles varied in the number of loops per whistle from zero to 17 loops per whistle with an average of 2.45 (± 2). Whistles also often contained harmonics of the fundamental frequency. The range in the number of harmonics was zero to three with an average of 0.5 (± 0.6).

Chirps rarely contained harmonics and were characterized by a constant frequency sweep; that is, they had no inflections or loops in the contour pattern (Fig. 17). Screams were frequency-modulated tones with "blurring" of the normally narrow-band frequency pattern (Fig. 18). Screams were difficult to classify to a particular contour type because of this

blurring. The blurring is possibly caused by aeration of the whistle during production (Fig. 18).

Click and Burst-pulse Vocal Types

Click trains, whines, and squawks were all comprised of a series of clicks apparently varying primarily in repetition rate. Repetition rates were variable both within and between different samples: constant, increasing, decreasing and any combinations of these three levels of repetition rates were observed (see click train examples in Fig. 19). Whines and squawks were characterized by repetition rates much higher as compared with click trains (Figs. 20 and 21). The variability in repetition rate within click trains could be caused by the angle at which the vocal dolphin and the hydrophones were positioned or by the change in swimming direction of dolphins approaching the camera and hydrophones. A third potential cause for the observed inconsistency in the repetition rate within click trains is that the dolphin may voluntarily be controlling this rate for communicative functions (see below). Specific frequencies for click vocalizations were not analyzed, but overall bandwidths were much wider when compared with the frequency-modulated tones. Estimated from spectrograms, click bandwidths ranged from about 9.1 - 18.3 kHz.

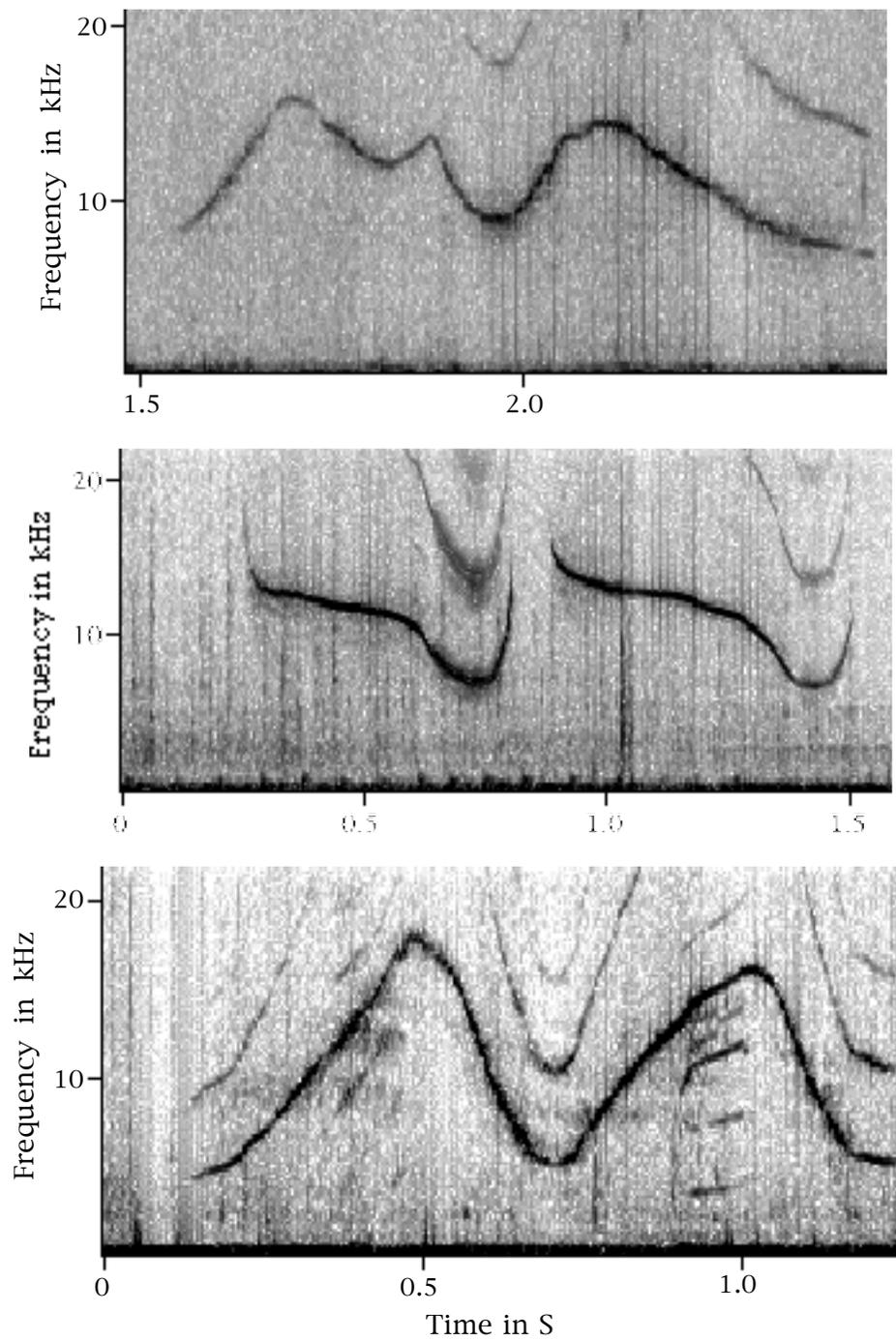


Figure 16. Spectrograms of example whistles. The third whistle given exhibits two loops.

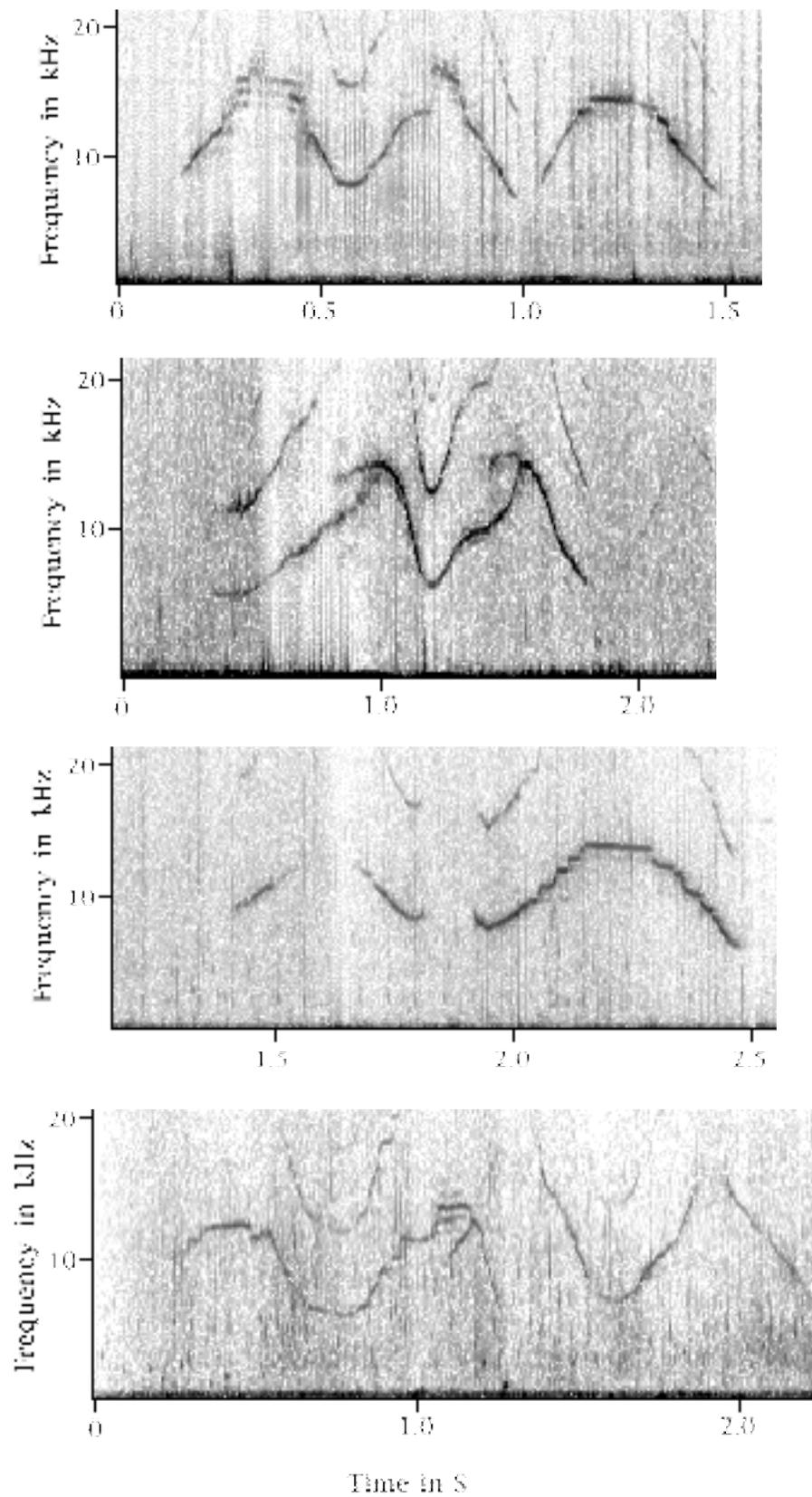


Figure 16. continued.

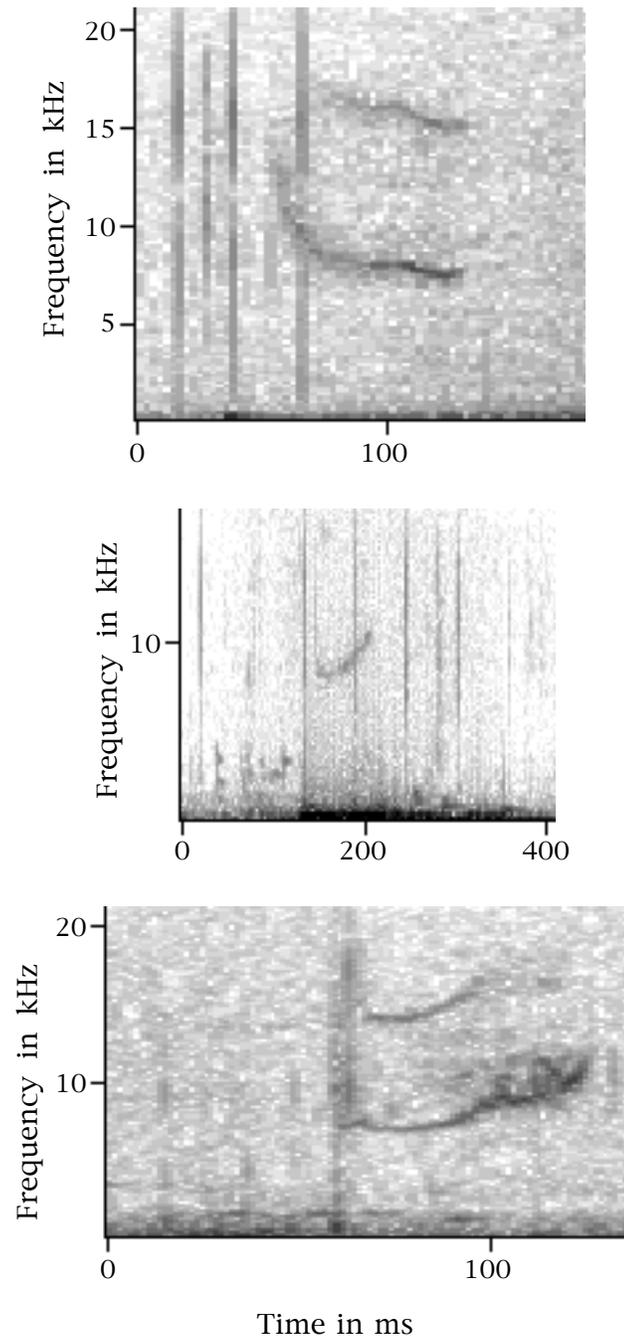


Figure 17. Spectrograms of three chirps vocalizations.

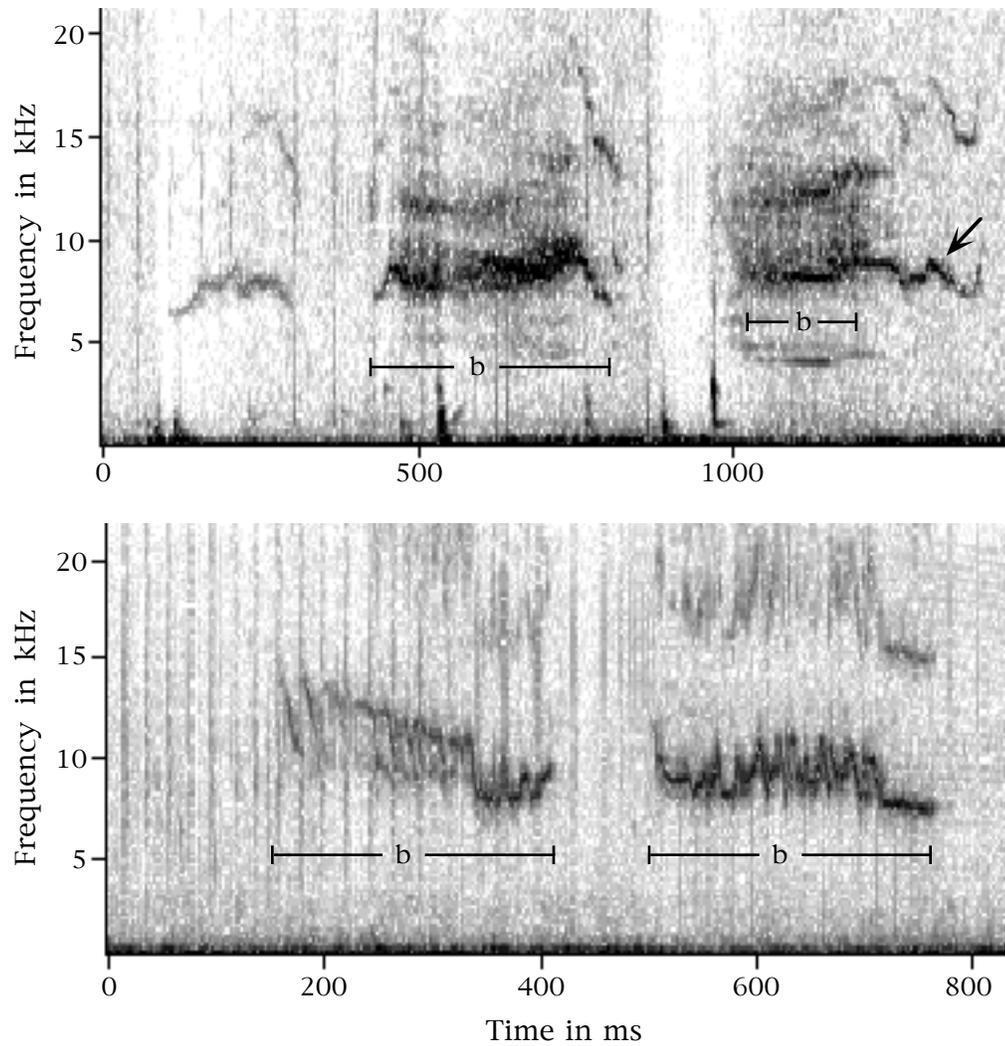


Figure 18. Spectrograms of two scream vocalizations. "Blurring" is indicated in both examples by "- b -". A segment of the narrow-band FM contour pattern is visible in the top example and is labeled with an arrow.

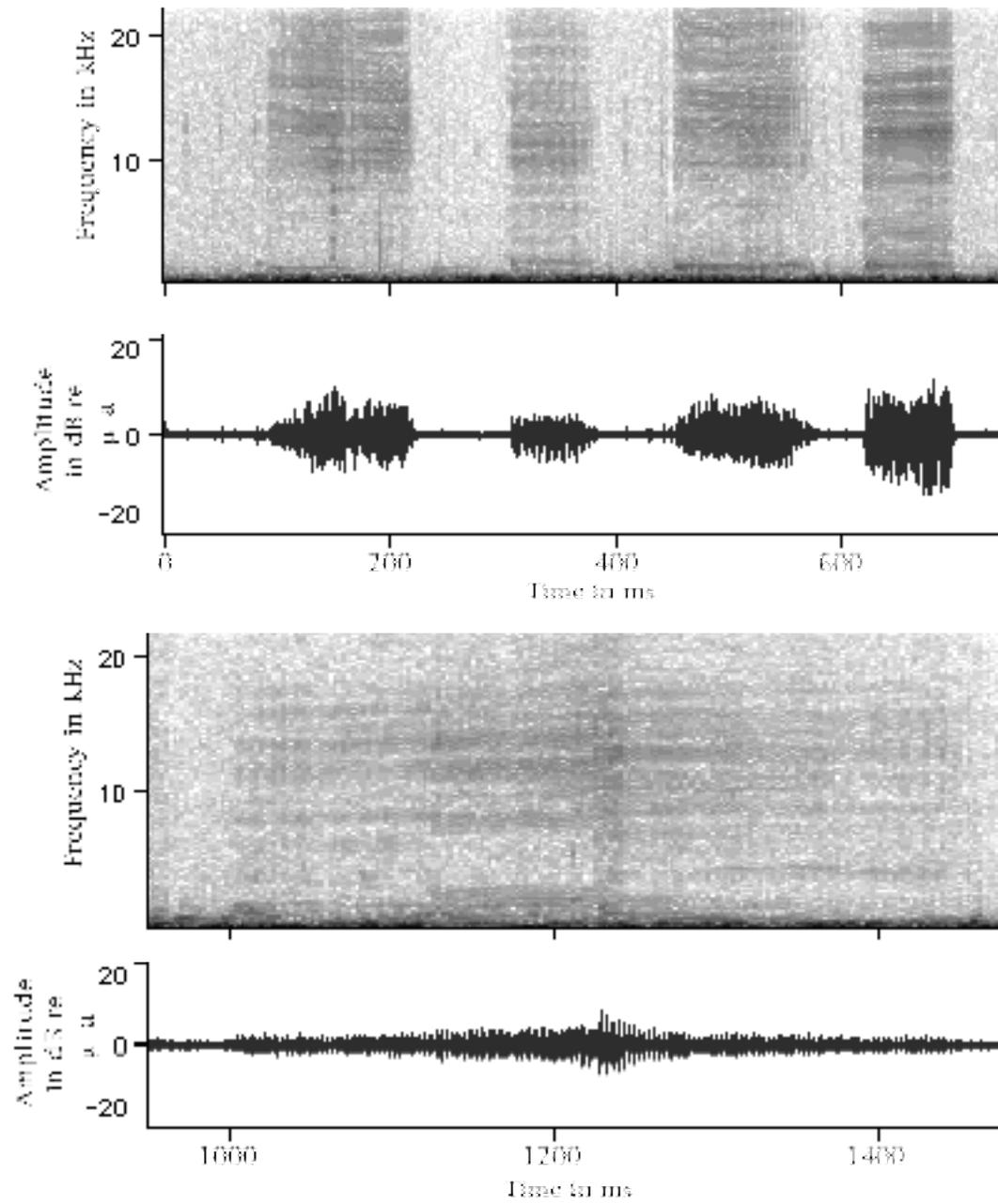


Figure 21. Spectrogram and waveform of two squawks.

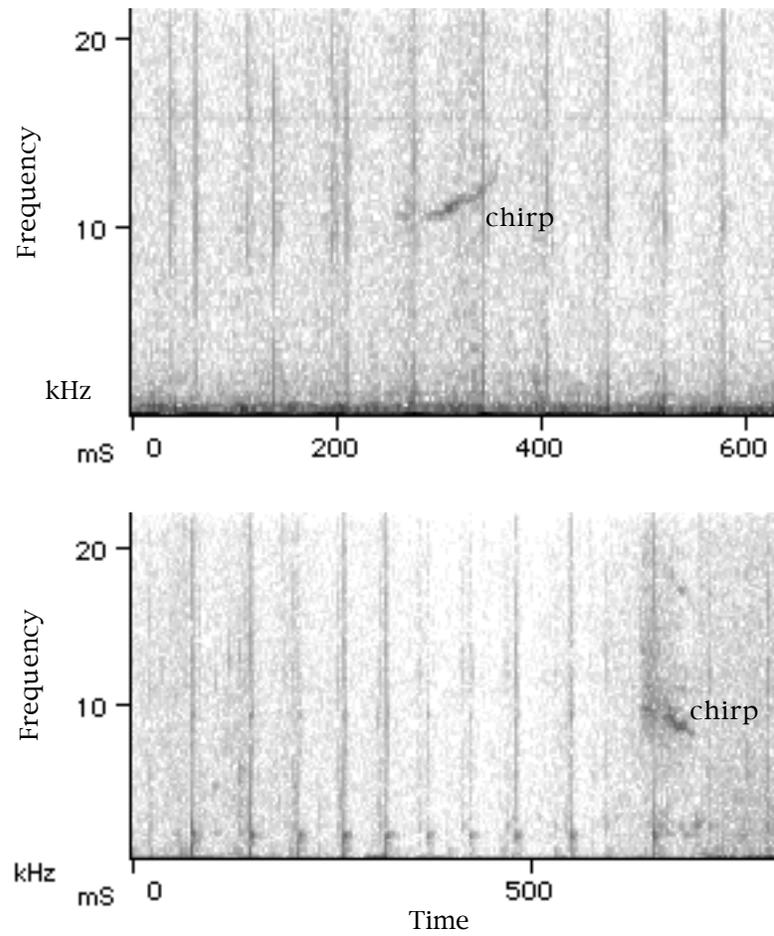


Figure 22. Spectrograms of a) two click-train/chirp and b) two click-train/whistle combinations.

Examples of Joint Vocal Types

Two or more vocal types were observed simultaneously on spectrograms of spotted dolphin sounds. For example, chirps or whistles concurrent with click trains were the vocal types most frequently documented together (e.g., Fig 22a, b). It is possible that one individual dolphin produced both vocal types (pers. observ.; Dr. William Evans, Texas Institute Of Oceanography, pers. comm. 1995). For about 50% of the chirps with click trains, the vocalizing dolphin could be identified, with the same dolphin producing both vocal types.

Other vocal types produced concurrently on spectrograms, and possibly from the dolphins, include, squawks, whines, click trains, and whistles, in almost any combination. During encounters where these vocalizations were recorded simultaneously, it was often not possible to localize the sound source direction or to determine the identity of the vocalizing individual (for example, see discussion of case study #94T6S6E1 below). These sounds were often recorded from several dolphins socially interacting in close proximity. Concurrent use of different vocal types and specific behaviors may have an enhanced communicative function.

VARIABILITY IN OCCURRENCE OF VOCAL TYPES

The vocal type observed in each of the five different behavioral activities (e.g., social) varied significantly from what was expected, with all χ^2 tests significant at $p < 0.001$ (Table 14). The number of whistles observed during play and social contexts largely contributed to the rejection of the null hypothesis (for this statistical test) that observed frequencies of vocalization types per context equaled the expected frequencies. Screams were not recorded during forage or travel activities of spotted dolphins, but were recorded more than expected in play and inquisitive activities (Table 14).

The observed number of clicks and chirps in play, and the observed number of squawks in forage were also examples of cells that were important contributors to the test results. Click trains and whines were observed significantly more than expected in play and much less than expected during social activities (Table 14). Click trains, however, are more directional than most other social sounds (Au, 1993), and therefore, might be under-

represented in the data due to recording vocal type directionality. The frequency range of recording equipment may also have been a limiting factor to the amount of click trains collected.

Table 14. Vocal types according to behavioral activity. Observed (obs.) and expected (exp.) values given for Chi square (χ^2) test analyses. See text for calculation of expected values. Inquis. equals the inquisitive context. "df" is degrees of freedom; "p" is the significance level.

BBC	VOCAL TYPE									
	whistles		chirps		screams		click-trains & whines		squawks	
	obs.	exp.	obs.	exp.	obs.	exp.	obs.	exp.	obs.	exp.
Social	428	350	110	117	3	7	92	136	81	66
Play	243	196	110	36	9	4	127	42	33	38
Forage	80	108	12	56	0	2	24	66	5	20
Travel	103	168	52	66	0	3	87	77	42	31
Inquis.	80	112	29	38	7	3	34	43	14	20
χ^2	70.2		48.1		18.9		102.5		58.2	
df	4		4		4		4		4	
p	<0.001		<0.001		<0.001		<0.001		<0.001	

Vocal types varied significantly according to group type, with all χ^2 tests significant at $p < 0.001$ (Table 15). The number of whistles observed from adult females with juveniles (AFjuv) and mixed groups were important contributors to the rejection of the null hypothesis for whistle variability with group type (Table 15). Click trains, chirps, and squawks were also observed more than expected from AFjuv groups. Squawks were never recorded from Mc groups and rarely from juveniles or same gender/aged groups. Screams were almost exclusively recorded from juveniles with an adult female and mixed groups (Table 15). Screams show a distribution in observed sample sizes similar to squawks.

Table 15. Vocal types according to group type. Group type abbreviations are given in Chapter II; others are the same as in Table 14.

GROUP TYPE	VOCAL TYPE									
	whistles		chirps		screams		click-trains & whines		squawks	
	obs.	exp.	obs.	exp.	obs.	exp.	obs.	exp.	obs.	exp.
AFjuv	335	216	140	65	16	4	165	81	65	41
juv	63	86	22	26	0	2	44	33	8	16
Mc	15	57	5	17	0	2	12	21	0	11
mix	466	424	89	127	3	9	93	160	94	80
same	47	143	21	42	0	4	35	54	7	26
χ^2	171.3		116.5		48.0		129.7		45.4	
df	4		4		4		4		4	
p	<0.001		<0.001		<0.001		<0.001		<0.001	

Vocal types varied significantly, but at different levels, with spot class (Table 16). Spot class (CL) 2 and CL3 produced more whistles than expected, while CL4 and CL5 were observed to produce fewer whistles than expected. Chirps were produced almost exactly as expected for CL2, CL3, and CL5, but much less than expected for CL4. Screams were only produced by CL2 and CL3 spotted dolphins (Table 16). Click trains and whines were produced by CL3 and CL5 more than expected but observed less than expected for CL2 and CL4. Squawks were observed significantly more from CL3 and CL4 when compared with CL2 and CL5.

Overall, CL3 and CL5 seemed more vocal than CL2 or CL4 (Table 16). These data represented an unbiased determination of the spot class of the vocalizing dolphin whenever the latter was identified. Caution should be taken, however, when comparing these values among group types and spot classes since spot class could not be determined for all recorded vocal types because the vocalizing individual was not always identified.

Table 16. Vocal types according to spot class. Abbreviations are the same as those in Table 14.

SPOT CLASS	VOCAL TYPE									
	whistles		chirps		screams		click-trains & whines		squawks	
	obs.	exp.	obs.	exp.	obs.	exp.	obs.	exp.	obs.	exp.
CL2	99	72	31	23	10	4	24	33	10	18
CL3	117	91	33	29	6	5	55	42	30	23
CL4	42	54	5	17	0	3	16	25	30	14
CL5	40	81	25	25	0	4	42	37	5	20
χ^2	41.0		11.8		16.2		10.4		35.24	
df	4		4		4		4		4	
p	<0.001		<0.05		<0.025		<0.001		<0.005	

VARIABILITY WITHIN WHISTLES

Nine contour types were most frequently observed from all recorded whistle and chirp vocal types (Fig. 23). A tenth category of contour types was labeled as "other" and included several multi-looped (using the Caldwell's definition for "loop" as an inflection point (Caldwell & Caldwell, 1968) contours that also had several breaks throughout the contour pattern. Types #1 and #2 were most frequently observed as chirps, but frequency-modulated vocalizations with a contour of type #1 or #2 that were longer than 500 ms were recorded and classified as whistles. These contour types represent a lumping of frequency-modulated vocalizations (excluding screams) based upon visual inspection of spectrograms. Further analysis of specific parameters (e.g., begin and end frequency, signal duration) may indicate a larger number of contour types based on usage by spotted dolphins or statistical clustering of measured variables.

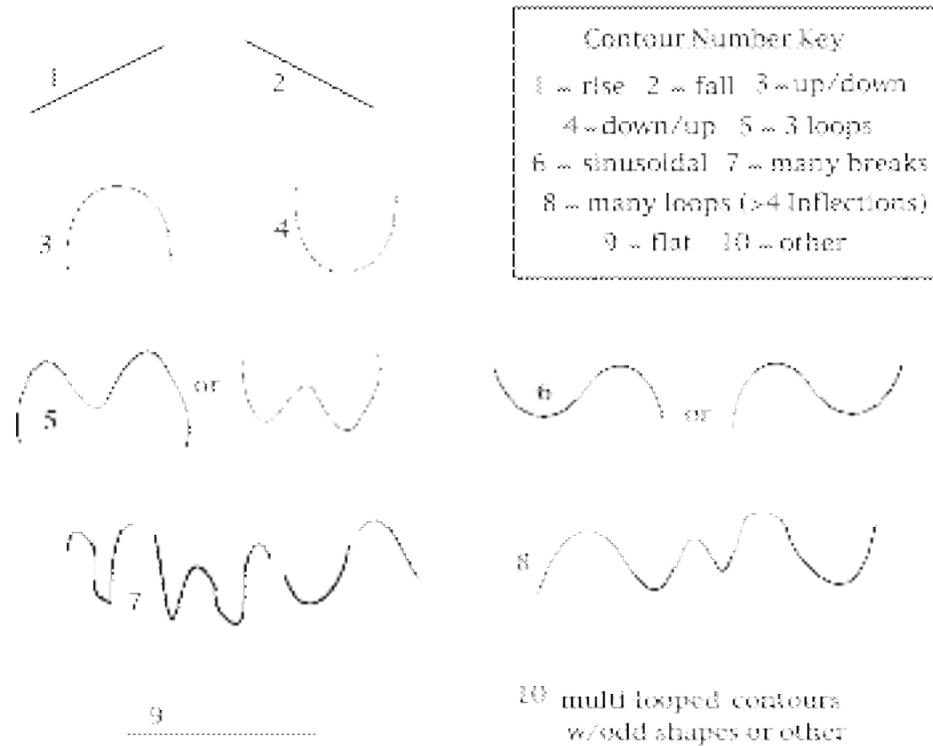


Figure 23. Schematic representations of ten different whistle and chirp contour patterns within the frequency-modulated vocal type. The number listed by each schematic is its "contour type number".

Contour types #3 and #4 were characterized by a single change in slope in the contour pattern. The initial rise and fall sections of whistles within these types varied in frequency bandwidth and duration but the general shape of the contour was conserved. Type #5 was characterized by three inflection points (or loops), while only two loops distinguish each type #6 contour pattern. The initial portion of the whistles within type #5 and #6 have either a rising or falling slope. Contour type #7 whistles had more than two loops, and generally were multi-looped in shape, but also had at least three breaks in the pattern; the breaks seemed to interrupt the path of the whistle. In some cases, manipulation of the spectrogram parameters highlighted and omitted the breaks on the contour. Thus, this actual contour type may be an artifact of the recording or analysis systems. Further analysis should clarify any discrepancies in the specific vocalizations categorized as type #7, but are currently beyond the scope of this work.

Whistles classified as type #8 were multi-looped with greater than four inflection points in the contour pattern. Several different patterns were recorded within this contour type with a sample of about 15 various multi-looped patterns. The vocalizing individual dolphin that produced many of these vocalizations was not identified. Thus, whether these whistle patterns represent individually distinct or behaviorally related vocalizations remains to be determined. However, since the number of patterns was relatively low ($n = \sim 15$) compared with the number of individuals within this study population, I suggest that these whistles are shared by many individuals.

All ten contour types (see Fig. 23) were produced by both genders and spot classes 2, 3, and 5: only type #9 was not recorded from class 4 spotters (Table 17). Whistles with two or more loops (types #5, 6, 8) were more frequently observed from all classes (36.3%) than type #1 or #2 contours (20.4%). Contours #1 and #2 were usually short in duration (< 500 ms), and mostly classified as chirps. More whistles were attributed to females ($n = 171$) than males ($n = 82$), but both genders exhibited similar distributions in production of the various contour types (Table 17).

All whistle contour types were recorded from adult females with juveniles, all juvenile, mixed and same group types (Table 18). Only contour types #1, #2, #4, #6, #9, and #10 were documented for groups of mothers and calves (Mc) (Table 18). Fifty percent of the whistles from Mc groups were of type #1: no multi-looped whistles were recorded from Mc groups. Contour #3 was the most frequently observed pattern observed during AFjuv (22.7%) and juv (20.4%) group types. A large number of multi-looped whistles were also recorded from these two group types (38.3% and 34.5%, respectively). A similar trend in the distribution of whistle contours was observed from same group types (Table 18). Type #1 was approximately 15% of the total number of whistles for both juvenile and same group types (Table 18). Mixed groups of spotted dolphins produced at least twice as many whistles as the other four group types (Table 18). Again, the majority of these whistles were multi-looped (46.0%), with rise contours (type #1) comprising the second most frequently observed whistle pattern (12.3%) from mixed groups.

Table 17. Occurrence and percentage of ten specific contour types of whistles according to spotted dolphin gender and spot class. Contour types are presented in Fig. 23, and correspond with the number listed in the "contour type" column. Numbers of contours summed for 1993 and 1994; percents given in parentheses. Male and female are abbreviated as "M" and "F", respectively.

CONTOUR TYPE	GENDER		SPOT CLASS			
	M	F	CL2	CL3	CL4	CL5
1	5 (6.1)	25 (14.6)	11 (14.3)	12 (10.2)	3 (8.3)	10 (17.2)
2	4 (4.9)	16 (9.4)	7 (9.1)	13 (11.0)	3 (8.3)	4 (6.9)
3	4 (4.9)	22 (12.9)	11 (14.3)	10 (8.5)	5 (13.9)	10 (17.2)
4	4 (4.9)	18 (10.5)	3 (3.9)	18 (15.3)	2 (5.6)	2 (3.4)
5	4 (4.9)	20 (11.7)	9 (11.7)	13 (11.0)	6 (16.7)	8 (13.8)
6	6 (7.3)	28 (16.4)	7 (9.1)	22 (18.6)	5 (13.9)	6 (10.3)
7	4 (4.9)	7 (4.1)	9 (11.7)	3 (2.5)	1 (2.8)	6 (10.3)
8	8 (9.8)	19 (11.1)	8 (10.4)	15 (12.7)	7 (19.4)	6 (10.3)
9	2 (2.4)	5 (2.9)	2 (2.6)	8 (6.8)	0 (0)	2 (3.4)
10	5 (6.1)	11 (6.4)	10 (13.0)	4 (3.4)	4 (11.1)	4 (6.9)
TOTAL	82	171	77	118	36	58

Table 18. Occurrence and percentage of ten specific contour types of whistles according to dolphin group type. See Chapter II for group type abbreviations, other abbreviations the same as indicated in Table 17.

CONTOUR TYPE	GROUP TYPE				
	AFJUV	JUV	MC	MIX	SAME
1	11 (8.6)	22 (15.5)	7 (50.0)	34 (12.3)	8 (15.4)
2	11 (8.6)	13 (10.2)	2 (14.3)	16 (5.8)	3 (5.8)
3	29 (22.7)	29 (20.4)	0 (0)	22 (7.8)	4 (7.7)
4	10 (7.8)	13 (10.2)	1 (7.1)	16 (5.8)	6 (2.2)
5	15 (11.7)	13 (10.2)	0 (0)	38 (13.8)	9 (17.3)
6	16 (12.5)	24 (18.8)	1 (7.1)	41 (14.6)	7 (13.5)
7	10 (7.8)	1 (0.8)	0 (0)	19 (6.9)	1 (1.9)
8	18 (14.1)	12 (9.4)	0 (0)	48 (17.4)	9 (17.3)
9	4 (3.1)	9 (7.0)	1 (7.1)	19 (6.9)	1 (1.9)
10	4 (3.1)	6 (4.7)	2 (14.3)	23 (8.3)	4 (7.7)
TOTAL	128	142	14	276	52

All whistle contour types were recorded from social, play, travel, and inquisitive behavioral activities (Table 19). Only contours with breaks (type #7) were not recorded from encounters labeled as forage (Table 19). Play was mostly characterized by type #3 (26.6%), although multi-looped contours represented a significant portion (30.3%) of whistles recorded during play. The distribution of whistle types in play is similar to that observed in juvenile group types (Table 19). The occurrence of multi-looped contours (37.8%) compared with non-looped patterns (35.4%) was almost equal during travel activities (Table 19). In contrast, the percent of non-looped contours (28.2%) was about half that of multi-looped whistle patterns (40.1%) during social activity of spotted dolphins (Table 19). Similarly, multi-looped whistles comprised a significantly larger sub-set (59.7%) of the total number of whistles during inquisitive activities as compared with non-looped contour patterns (13.9%).

Table 19. Occurrence and percentage of ten specific contour types of whistles according to behavioral activity.

CONTOUR TYPE	BEHAVIORAL ACTIVITY				
	SOCIAL	PLAY	FORAGE	TRAVEL	INQUIS.
1	41 (13.3)	15 (13.8)	5 (11.9)	15 (18.3)	6 (8.3)
2	20 (6.5)	7 (6.4)	3 (7.1)	11 (13.4)	3 (3.7)
3	42 (13.6)	29 (26.6)	3 (7.1)	3 (3.7)	9 (11.0)
4	16 (5.2)	4 (3.7)	7 (16.7)	12 (14.6)	4 (4.9)
5	38 (12.3)	12 (11.0)	8 (19.1)	5 (6.1)	13 (15.9)
6	44 (14.2)	15 (13.8)	5 (11.9)	13 (15.9)	14 (17.1)
7	14 (4.5)	5 (4.6)	0 (0)	8 (9.8)	3 (3.7)
8	42 (13.6)	16 (14.7)	5 (11.9)	10 (12.2)	16 (19.5)
9	26 (8.4)	2 (1.8)	3 (7.1)	3 (3.7)	1 (1.2)
10	26 (8.4)	4 (3.7)	3 (7.1)	2 (2.4)	3 (3.7)
TOTAL	309	109	42	82	72

QUALITATIVE SOUND OBSERVATIONS

Spotted dolphin vocalizations varied in type (e.g., squawks, whistles); their sounds also varied in occurrence (i.e., number of vocalizations per type) and intensity according to context, referents, and individual. It was difficult (if not impossible) to quantify intensity because the distance between the vocalizing individual and the hydrophones could not be kept constant and because the dolphin might not always face directly at the hydrophones. Intensity and rate increased during heightened social activity, especially when aggressive behaviors (e.g., HTH, JCP, RAM, see Appendix C) were exchanged among individuals. Squawks were "hard" or intense vocalizations with much energy and were recorded primarily during aggressive or play interactions from interacting juveniles and subadults. Click trains produced by spotters were recorded mainly during approaches or during 'inquisitive' behaviors, such as approaches to others and play with objects. The high repetition click trains or whines, were produced largely by younger dolphins when excited or during play.

Screams were only recorded from young dolphins (calves and juveniles) and were often accompanied by fast swimming around snorkelers and conspecifics: these individuals seemed to be excited. Occasionally, a partial contour was evident in a scream (Fig. 24). Recognizable contours or partial contours lend evidence to the idea that screams may actually be whistles accompanied by extra air during vocalization. That is, the whistle or frequency-modulated contour is "over-produced" thus causing a "blurring" of the contour pattern (Fig 24). The frequency-modulated tone then is expressed with a "screechy" quality sounding very much like a scream to the human observer.

Spotted dolphin whistles vary more with behavioral activity and associates than with particular individuals or individual gender (Table 20). Whistles were recorded from all spot classes and during every behavioral activity. Similar to the squawks, whistles seemed to increase in intensity during socially aggressive encounters. This information should be taken as anecdotal, however, since only three aggressive encounters were recorded during the study period. This observed variability in spotted dolphin whistles does not preclude the presence of individual characteristics. My sample size of whistles for specific individuals across more than one or two behavioral

contexts is quite limited (Table 20). But based upon information available from captive and free-ranging spotted dolphins (Caldwell *et al.*, 1973; Herzing, 1994), I agree that spotted dolphins possess individually distinct whistles. Whether the individually-distinct quality to spotted dolphin whistles is represented in the contour pattern or in other measurable parameters of whistles remains to be analyzed for this study group.

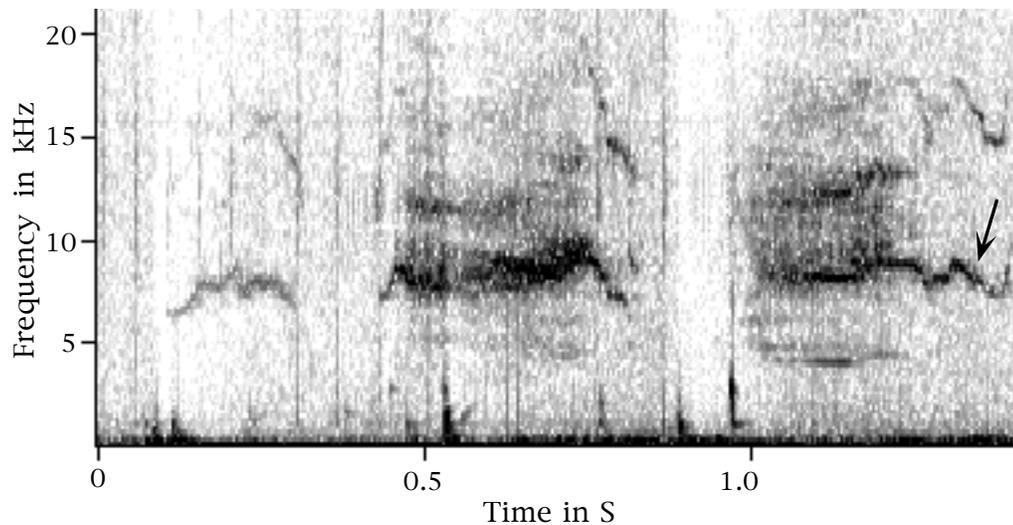


Figure 24. A scream with evidence of a partial frequency-modulated contour pattern. FM pattern indicated with an arrow.

Within-Individual Variability

For 37% all sounds recorded and analyzed, the vocalizing dolphin was identified: specifically, identification was verified for 37.0% of the whistles, 30.0% of the chirps, and 45.1% of the click trains and whines. The percent-identified is low for chirp sounds: chirps are often produced when two dolphins are within two body widths of each other and at least five meters from the camera and hydrophones, making it difficult to determine which dolphin is vocalizing. Click trains are more directional and are recorded mainly when dolphins were approaching the MVA system; therefore, an increase in the percent of identified vocalizing individuals would be expected because of the animal's behavior. Individuals producing squawk sounds were not identified; squawks were usually produced in socially active groups

where individuals were often in close proximity to one another. Class 2 and class 3 spotted dolphins produced all screams recorded. The former were often not re-identifiable and thus, identity of the vocalizing individual was not determined.

While sample sizes were not large enough for quantitative statistical calculations on all individuals identified as the vocal animal, individuals from this group of spotted dolphins produced a variety of whistle types (Table 20). Females and males did not appear different in their variety of whistle types produced (Table 20). One individual male spotter (#112, Table 20) produced many more whistles of type #3 than of any other contours. This male produced these whistles during one encounter while fast-swimming in tight circles around another male dolphin and one snorkeler. Similarly, dolphin #109 produced more type #5 and #6 whistles than any of the other contour patterns (Table 20). Still, most of the other spotted dolphins did not exhibit an affinity to a particular whistle contour. More data are required to statistically investigate whether members of this spotted dolphin group possess individually-distinct whistle contour patterns. It is possible that spotted dolphins also preferentially use certain whistle types depending on behavior or group composition; however, more data are required to address these questions.

Table 20. Whistle contour variability for selected individual spotted dolphins. See Fig. 23 for whistle pattern contour types. Sample sizes for each contour type per specific individual dolphin given in parentheses. Males listed in left column; females listed in right column.

<u>ID#</u>	<u>contour types</u>	<u>ID#</u>	<u>contour types</u>
9	#1 (2), #4 (2) #5 (3), #6 (2) <u># 8 (2), #10 (1)</u>	45	#1 (1), #3 (2) #3 (2), #4 (1) #5 (3), #6 (2) <u>#8 (2), #10 (2)</u>
12	#2, (1), #3 (2) #5 (1), #6 (1) #7 (1), #9 (1) <u>#10 (2)</u>	61	#1, (2), #2 (1) #3 (3), #5 (1) #6 (1), #8 (2) <u>#10 (3)</u>
80	#1 (1), #4 (1) #5 (1), #6 (2) <u>#10 (2)</u>	93	#1 (4), #2 (3) #3 (1), #4 (1) #6 (4), #8 (1) <u>#10 (4)</u>
94	#1 (5), #2 (1) #3 (6), #4 (7) #6 (3), #8 (2) <u>#10 (1)</u>	109	#1 (3), #3 (1) #4 (1), #5 (6) #6 (6), #8 (1) <u>#10 (2)</u>
97	#1 (2), #3 (1) #4 (1), #5 (3) #6 (1), #8 (2) <u>#10 (1)</u>	111	#1 (1), #4 (2) #5 (2), #6 (1) #8 (4), #9 (1) <u>#10 (3)</u>
112	#2 (1), #3 (11) #5 (6), #6 (3) <u>#8 (2), #9 (1)</u>		

A Case Study: Encounter #94T6S6E1

The case study - encounter #94T6S6E1 - was described in behavioral detail, with reference to the amount and type of vocalizations produced, in Chapter III (Table 21). A more specific description of the acoustic behavior of dolphins involved in this encounter is given in Table 21. This encounter was characterized by alternating bouts of aggressive and affiliative behavior (see Table 12, Chapter III). Vocal activity varied with changes in tactile and aggressive actions. At the beginning and end of this encounter, the dolphins were audible, but not visible to us. Squawks, whistles, click trains, and other loud vocalizations (e.g., underwater jaw claps and tail slaps) were recorded. Bubble emissions (e.g., streams, trails, clouds) were prevalent during segments with heightened vocal activity. More descriptive acoustic detail is

given in Table 21; example spectrograms for four sections from this encounter (ranging from 1.0 to 6.5 seconds in length) are given in Fig. 25.

Table 21. A description of acoustic activity, with a minimal discussion of associated behaviors, from encounter #94T6S6E1. Screen-time is real time for encounter.

<u>SCREEN-TIME</u>	<u>ACOUSTIC DESCRIPTION</u>
12:29:34	START RECORDING. SOUNDS AUDIBLE: SQU, WHS, ECC
12:29:45 - :51	MUCH VOCALIZATIONS, MULTIPLE DOLPHINS CKW INTO VIEW
12:29:58	VOCALIZATIONS SEEM TO INTENSIFY AS INTERACTIONS ESCALATE: MUCH SQU, BBT, BBC, WHS, JCP
12:30:00	VOCALIZATIONS TAPER OFF, BBB BY ONE THEN ANOTHER DOLPHIN. HTH
12:30:11	ANOTHER BBB BY THIRD DOLPHIN. INTENSE SQU, WHS
12:30:33	C4 SWIMS TO LEFT, OTHERS FOLLOW W/ECC, SQU, WHS, BBB
12:30:40	WHS, SQU, ECC, WHINES, BBB
12:31:10	FSW ALL OUT OF VIEW.
12:31:35-:57	WHS, SQU, ECC, WHINES AUDIBLE BUT NO ANIMALS IN VIEW
12:32:36	NO SOUNDS AUDIBLE
12:35:25	AGGRESSIVE INTERACTIONS. MUCH SOUNDS: SQU, WHS, ECC BBS & BBT, RAM, HIT, JAW, JCP
12:36:15	SQU, WHS, SRB, LOB, NDG, PUU, PDD
12:36:49	START VOCALIZING AGAIN (ALL VOC.'S); LOB, GAB
12:37:13	JCP, SQU (CL3 TO CL3) NEAR LOB, GAB
12:37:29	START AGAIN
12:37:45	BBS, WHS BBC, BBT
12:38:05	HTH, & AWAY IN FSW, SPIRALS; SOUND STILL AUDIBLE
12:38:40	END ENCOUNTER

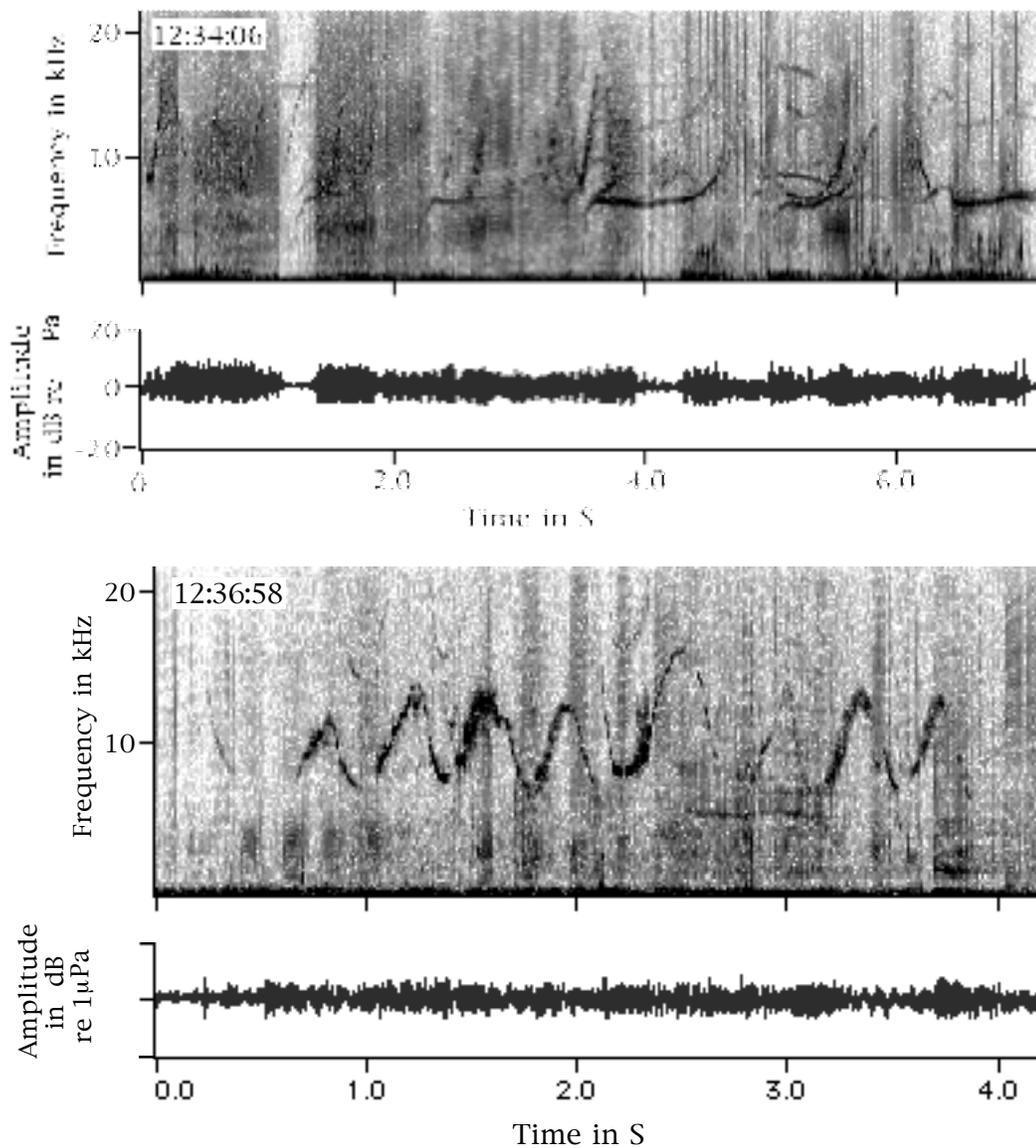


Figure 25. Spectrographic examples of the vocalizations heard and recorded during encounter #94T6S6E1. Squawks, whistles, click trains and other sound types are included in these examples. Screen time (i.e., real time) listed below each spectrogram for reference to Table 21.

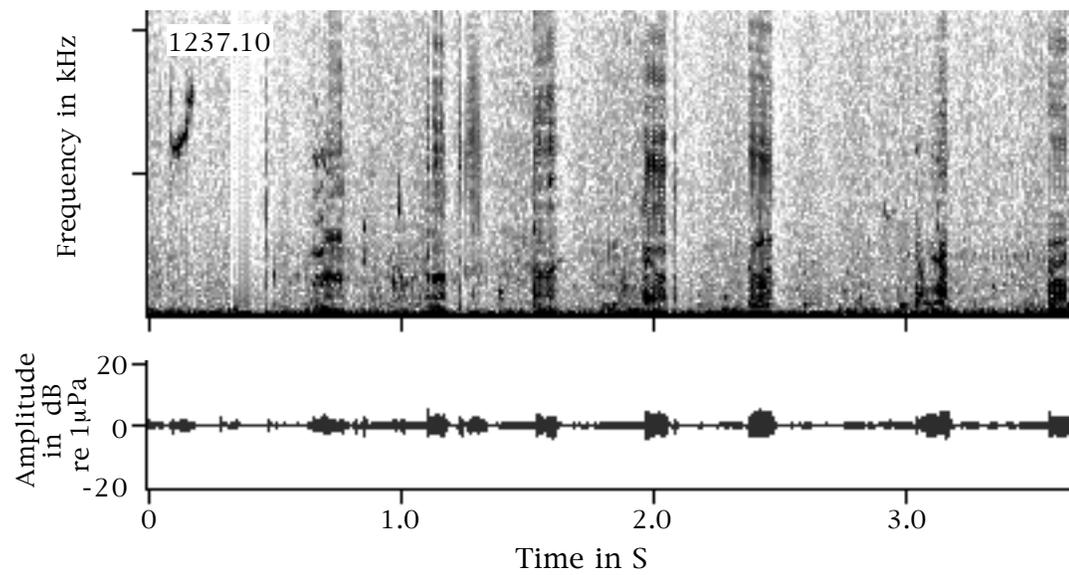
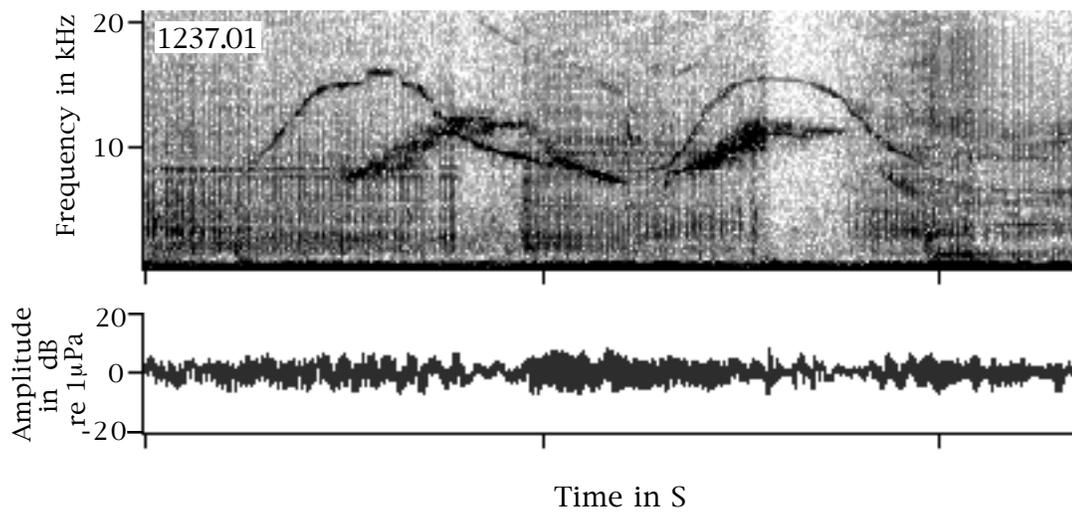


Figure 25. continued.

Non-Videotaped Encounter Data

In general, social and play contexts were characterized by a greater number of whistles. Click trains were noted primarily when individual dolphins seemed inquisitive of snorkelers or other objects along the sea floor. Screams and squawks were observed and documented more during excited activity, usually exhibited by juveniles and calves engaged in fast swimming around other dolphins and humans. These observations must be viewed with caution as they may also reflect the participant/recorder's bias while documenting what was just previously experienced underwater. Still, the notes seem to indicate a high degree of accuracy when examining the level of vocal activity as related to the level of behavioral activity documented, and also when compared with statistical analyses on recorded vocal types per encounter, group type, and spot class (see above).

Two specific examples of spotted dolphin vocal behavior warrant inclusion and comment in this section. During at least five different encounters in 1993 and 1994, I observed a spotted dolphin calf swim tight circles around one to three passengers or dolphins, while emitting an audible, stereotyped whistle. This behavior immediately preceded the encounter end because the calf swam out of our view after whistling. On two occasions, within a few minutes of the encounter end, the stereotyped whistle was again audible but the calf did not swim back into view. During the four years of my project, volunteer participants observed and recorded this same behavior by class 2 spotted dolphins in at least six encounters, separate from the ones I described above. It is not possible to determine if the calf was joining other individual dolphins since observations were from underwater and usually at least 10 m from the boat. Although the audible whistle was familiar, it was not possible to determine if this whistle was a particular contour type (see Fig. 23) repeated again and again; or if the whistle was a variant of the multi-looped contour patterns (e.g., type #8). Nonetheless, the whistles were stereotyped to the human listener.

Second, anecdotal and recorded evidence support the shared use of at least one complex whistle contour. Three different individual spotted dolphins, representing both genders and three spot classes, produced a very distinctive whistle (Fig. 26). This whistle was produced by spotted dolphins #61, #111, and #12 -- the latter an adult male, #61 a subadult female, and #111

a juvenile female (see Appendix A). When recorded from each individual, the other two dolphins were not within view, nor were they involved in an encounter for at least four hours from the previous recording of the whistle. In fact, this whistle was recorded from #61 in 1993 and 1994, from #12 in 1994 and from #111 in 1994. Each individual produced this whistle during a different behavioral activity and with a different group composition, although some associates were the same among these group types.

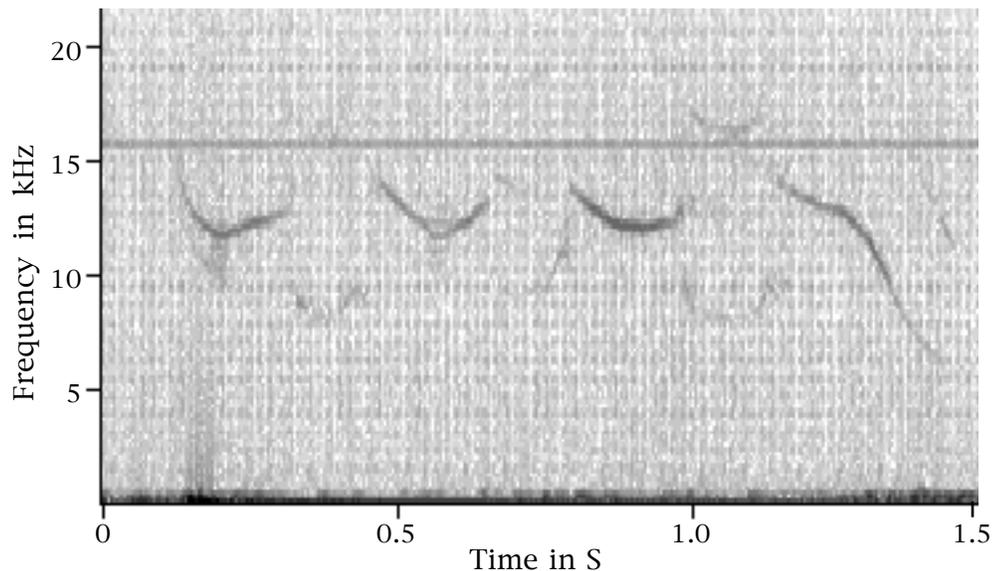


Figure 26. Whistle produced by three spotted dolphins differing in age and gender.

DISCUSSION

In water, sound is often a more reliable means of exchanging signals than visual displays or posturing. While our knowledge of the types of sounds produced by cetaceans is extensive (e.g., Worthington & Schevill, 1957; Caldwell & Caldwell, 1965; Backus & Schevill, 1966; Evans, 1967; Payne & McVay, 1971; Tyack, 1976; Clark 1990), relatively few studies have examined the biological significance or use of sounds in whales and dolphins (e.g., Clark, 1983; Tyack, 1983; Silber, 1986; Sjare & Smith, 1986; Weilgart & Whitehead, 1990; Smolker *et al.*, 1993; Sayigh *et al.*, 1995). This Chapter focuses on the variety of sounds produced by a group of Atlantic spotted

dolphins, as well as the occurrence, and potential functions, of these vocalizations according to varying behavioral activities, group compositions, and individual gender, age or identification.

VOCAL TYPES

Spotted dolphins in this study produced several vocal types similar to what has previously been reported for captive and free-ranging spotted and bottlenose dolphins (e.g., Caldwell & Caldwell, 1971; Caldwell *et al.*, 1971, 1973; Tyack, 1976, 1986; Caldwell *et al.*, 1990; Sayigh, 1992; Herzing, 1994). These vocal types are frequency-modulated tones, or whistles, chirps, and screams; and pulsed or click sounds including click trains, whines, and squawks. Spotted dolphins were also heard to make noise behaviorally during contact with conspecifics, including body slams or slaps, jaw claps, and splash sounds upon water re-entry.

Frequency-Modulated Tones

While whistles were probably not recorded from all individuals within this study population, they were audible from all spotted dolphins encountered during this four-year study. In general, whistle duration and frequency bandwidth were similar in range to values reported previously in the literature (e.g., Caldwell *et al.*, 1973; Herzing, 1994). Duration and frequency ranges were not analyzed in detail, however, because the scope of this portion of my work was to investigate occurrence (or use) of vocal types according to dolphin behavioral activity, group composition, and individual. Specific contour patterns of whistles, based upon the spectrogram of each frequency-modulated tone, are discussed below.

The number of loops and harmonics present in whistles has been used to denote complexity in dolphin whistle structure (Caldwell & Caldwell, 1971, 1973; Tyack, 1986b; Wang, 1993). The range in number of loops and harmonics found in the whistles of this group of spotted dolphins are consistent with previous work suggesting that spotted dolphin whistles are more complex when compared with bottlenose dolphin whistles (Caldwell *et al.*, 1971; Wang, 1993). Structural complexity in vocalizations may be an important factor in species recognition among groups of two sympatric species (Alcock, 1988; Grier & Burke, 1992). For example, male swamp

sparrows failed to learn songs of the sympatric song sparrow (Marler & Peters, 1977). Differences in whistle structure may be necessary in the Bahamas where spotted and bottlenose dolphins share habitat ranges (pers. observ.; Rossbach, 1995). Data on bottlenose dolphin vocalizations in this location are needed. A future comparison of data on bottlenose and spotted dolphin whistles from this area would provide information to address the issue of whistle complexity differences among two different, but sympatric, dolphin species.

Whistles, or frequency-modulated tones in general, are thought to be the primary communicative vocal signal among delphinids (Evans & Bastian, 1969; Herman & Tavolga, 1980). Whistles were recorded during all behavioral activities and from all group types of spotted dolphins. The majority of these tones were recorded during play and social activities as compared with encounters characterized by travel, forage, or inquisitive activities. An individual dolphin can be in active physical contact with one or two dolphins at a time, but can vocally communicate with all individuals in an encounter (or group) simultaneously. Conversely, the observed number of whistles was lower than expected during travel, forage and inquisitive activities, suggesting that when dolphins are engaged in non-interactive behaviors there is less need to communicate among individuals. Still, whistles were not non-existent during these activities, indicating that even some aspects of the activities of single individuals may be worth sharing with other group members. For example, dusky dolphins were recorded to produce whistles when traveling in small groups separated by about one kilometer (Würsig & Würsig, 1980); these small groups were often observed to join and feed on large schools of fish.

Chirps were recorded primarily when individual dolphins approached conspecifics after separations in time and space. Chirps were also emitted by spotted dolphins during play contexts when individuals were involved in much contact and engaged in behaviors that were also observed during aggressive behavioral contexts. However, chirps were not recorded during aggressive social activities. Chirps may therefore be a vocal cue among dolphins that the ongoing activities are "not serious"; that is, play is the dictate of activity among conspecifics.

Screams, the third frequency-modulated type of sound, were raspy, breathy sounds. A blurring of the fundamental frequency is probably caused by air escaping through the blowhole while vocalizing, hence, the raspy quality to this sound. Screams were recorded only from juveniles and calves primarily during play and social contexts while among other juveniles (or calves) and one or two adult female spotted dolphins.

The vocal signals of spotted dolphins may convey information and establish communication among individuals. Screams and squawks probably convey much referential information to conspecifics, including excitement level or agitation. Screams were produced only by young spotters during play or social activity; during these contexts, young dolphins were engaged in much fast and circle swimming, which is usually indicative of excited behavior (Caldwell & Caldwell, 1971).

Click and Pulse Sounds

Spotted dolphin clicks were much shorter (less than 100 ms) than frequency-modulated sounds. Clicks were usually produced in series to form click trains, whines, and squawks. A detailed examination of click and interclick durations was not conducted during this study; however, interclick durations seemed to vary between the three categories of click sounds to yield varying repetition rates. While click trains and whines were grouped during analyses due to low sample sizes, it is probable that these two types of vocalizations have different functions among interacting dolphins. Click trains and whines were recorded during significantly different intraspecific interactions when compared with squawks.

Click trains seemed to be associated with inquisitive behaviors by dolphins. Individuals often produced click trains when approaching the camera and researcher or other snorkelers. Click trains were also audible when dolphins were digging in the sand on the bottom with their rostrums. Occasionally, during the latter incidents the dolphins were observed to grasp, and subsequently ingest, a fish in their mouth. These documented events suggest a function for click trains, while the inquisitive behaviors associated with some click trains might indicate a more communicative reason behind click production. This does not preclude that these clicks are primarily the low-frequency component of echolocation clicks. Whines were audible more

from juveniles during play activities. Whines were characterized by much higher repetition rates than click trains. Whines from spotted dolphins are similar to cries from Hector's dolphins (*Cephalorhynchus hectori*, S. Dawson, pers. comm. 1996). Hector's dolphins do not produce frequency-modulated tones, but modify their pulsed vocalizations depending on group activity and size (Dawson, 1991). Although the communicative function for click sounds has not been studied in much detail in dolphins generally, a communicative function cannot be ruled out (Herman & Tavolga, 1980).

According to Dawson (1991), Hector's dolphin cries were associated mainly with aerial and aggressive behaviors. Since all observations in Dawson (1991) were from the surface while recording sounds, an indication of the age or identification of the vocalizing individuals was not possible. For spotted dolphins, the whines were produced by all classes but predominantly by juveniles during very physically active play and social modes. Between both species, the activities could be considered similar in level of activity. Thus, high repetition pulse rates, and resulting vocalization types, may be indicative of the level of activity, as well as the type of interaction for all dolphin species that modify repetition rates and signal durations.

Squawks are pulsed vocalizations with a repetition rate much faster than dolphin whines. The individual clicks or pulses of squawks are not audible to the human ear when compared with the 'rusty hinge' quality of click trains. Qualitatively, squawks have harsh, abrupt, acoustic characteristics. Jaw claps, hits, head-to-head postures, and tail hits were all associated with squawking in spotted dolphins. Squawks may express irritation or anger among and between vocalizing dolphins (e.g., see Tables 12 and 21). Within the framework of Morton's hypothesis of motivation-structural rules in vocal behavior (Morton, 1977, 1982), I suggest that squawks from spotters fall distinctly on the hostile end of the gradient. Squawks were recorded primarily from class 3 and 4 spotters during agonistic and aggressive social interactions.

Squawks, or harsh vocalizations, may be indicative of more agonistic interactions among individual dolphins. Marten *et al.* (1988) and Caldwell and Caldwell (1971) reported squawks and other loud pulsed sounds from bottlenose dolphins during aggressive displays. These vocalizations may be a less harmful way of communicating anger or agitation as compared to

physical contact. Dolphins are capable of inflicting deadly damage to conspecifics (e.g., Wilson, 1995); thus, it would be cost effective in terms of energy expended for individuals to use non-physical means to express anger as opposed to inflicting physical damage to conspecifics.

Squawks were not recorded from mother/calf groups but were primarily heard from mix groups of juveniles and subadults during social interactions. Use of harsh sounds (such as squawks) coupled with physical expressions of agitation (e.g., tail hits) may establish the biological function of such vocalizations.

Joint Vocal Types

Clicks in delphinids are thought to be produced when a dolphin passes air over the dorsal bursa located within its skull (Cranford, 1992). The exact location of whistle production is not established with certainty. Whistles are thought to be produced by the exchange of air among the internal nasal air sacs of dolphins (Norris, 1967; Evans & Prescott, 1975; Curry, 1992). Thus, it is possible that a single dolphin could produce both click and frequency-modulated sounds simultaneously. Spotted dolphins were observed to produce both click trains and whistles and click trains and chirps simultaneously. These vocalizations were recorded primarily from individuals approaching conspecifics, snorkelers or the camera, and are thought to be inquisitive in function. The click train could represent an inquisitive or searching function, while the chirp may indicate a non-threatening message. Similarly, a whistle may indicate contact or social cohesion. Further data are required to address the possible uses or functions of joint vocal types.

VOCAL TYPE VARIABILITY

Production of vocal types in this group of spotted dolphins varied according to behavioral activity, group type, and spot class of the vocalizing individual(s). Whistles, chirps, click trains (and whines), and squawks were produced during all behavioral activities by all age classes, but to varying degrees, suggesting that vocal behavior is linked with activity. The number of vocalizations of all vocal types increased when spotted dolphins were engaged in social activities, but did not reflect the increased group size for most social activities. Mixed groups were larger on average than other group

types (see Chapter III), but mixed groups were not the only groups engaged in social activities. Adult female(s) with juvenile groups (AFjuv) and mixed groups of spotted dolphins were observed primarily engaged in social, play, and travel activities (see Chapter III). These two group types were observed to produce the majority of the recorded vocalizations, especially whistles, chirps and squawks, during this study. Variety in vocal types recorded was larger for groups of spotted dolphins engaged in more active encounters, such as social and play. Similar trends in vocal behavior were observed for beluga and pilot whales, although the rate of vocal activity also varied with group size for these species (Sjare & Smith, 1986; Weilgart & Whitehead, 1990).

Sayigh *et al.* (1990) and Sayigh (1992) provided evidence supporting the development of signature whistles in a free-ranging population of bottlenose dolphins in Sarasota Bay, Florida. They showed that signature whistles were not determined exclusively by genetics. Whistle contours were learned, and included effects of the early social and auditory environments (Sayigh, 1992). The individual contours were relatively stable by one year of age and showed differences in development between female and male calves when compared to the signature whistle of the assumed mother (Sayigh *et al.*, 1990). Reiss and McCowan (1993) examined whistle contour development in captive-born bottlenose dolphins and found that primarily two whistle types were shared by all calves across all social groups. Ontogenetic changes were found by the authors in the structure, use, and context of whistle type from calves: vocal plasticity and learning were suggested in the use of whistle vocalizations by bottlenose dolphins by Reiss and McCowan (1993) because of the use of whistles according to context by calves. These results are similar to studies of the ontogenetic development of alarm calls in vervets (Seyfarth & Cheney, 1980).

DIFFERENCES IN WHISTLE CONTOUR PATTERNS

The presence and use of individually distinct vocalizations for sperm whales were first suggested by Backus and Schevill (1966), but Weilgart and Whitehead (1993) showed that signature codas were not produced by sperm whales in the Galapagos population. They documented only 23 codas for a population of over 400 sperm whales. Evidence of individually distinct (or

signature) whistles in dolphins was first documented by Caldwell and Caldwell (1965). Caldwell *et al.* (1973) presented evidence that captive spotted dolphins produced signature whistles, although the distinction in their whistles was less pronounced as compared with bottlenose dolphins. More recently, Herzing (1994) suggested that the Atlantic spotted dolphins in northern Bahamian waters produced signature whistles; however, Herzing did not include spectrograms or describe her methodology for classifying specific whistles to particular dolphins. My data suggest that spotted dolphin vocal behavior, and the dolphins' use of all types of vocalizations, varies more as a function of behavioral activity, group type, and spot class than individual.

Support for the prevalent use of signature whistles is not found in my data: within the 10 given contour types, a maximum of 15 specific contours were identified from this group of at least 95 individual spotted dolphins. Each of these contours was produced by at least five different individual spotted dolphins. No individual spotted dolphin produced one specific contour faithfully to the near exclusion of any other pattern. These results are similar to the findings of Weilgart and Whitehead (1993) for sperm whale coda communication. From recordings and observations of a population of about 400 sperm whales off the Galápagos Islands, only 23 coda types were discovered (Weilgart & Whitehead, 1993). The authors also found that different coda types were emitted by the same individual, while many different individuals were recorded using the same codas. The latter case was also observed for sperm whales in the Caribbean Sea (Watkins *et al.*, 1985).

Weilgart and Whitehead (1993) suggested that the most probable function of codas was to maintain social bonds among conspecifics. This is certainly the case with some primate calls (e.g., Boinski, 1993). Since whistles were primarily recorded from spotted dolphins during social and play activities with mixed group types, maintenance of social bonds is also the most likely function of general whistle use among these dolphins.

From approximately 20 hours of tape that yielded 934 whistles for analysis, only 10 general whistle contour types were observed. Admittedly, variation in whistle patterns is probably greater than the 10 contour types defined for my study. For example, there was variation in the multi-looped contour categories, but specific whistles were not identified to certain

individuals. Also, caution is recommended when interpreting all whistle data because all recordings were made underwater during encounters while dolphins were swimming over a shallow sand bar. Thus, assuming that the signature whistle is part of a larger vocal repertoire of an individual, it is possible that my data may not reflect situations when dolphins may most use their signature whistles.

This does not, however, negate the effects or potential use of individually distinctive characteristics that may be found within a specific dolphin's vocalizations. Signature whistles may not have a broad use or application in this group of spotted dolphins: it is possible that spotted dolphins rely more on visual cues for identification (e.g., spotting patterns). The clear water would permit use of such characteristics. A comparison specifically examining the rate of vocal activity to behavioral activity as compared to the water clarity might provide information to answer this question.

The Atlantic spotted dolphins are assumed to at least possess signature whistles based upon data from captive studies (e.g., Caldwell & Caldwell, 1971; Caldwell *et al.*, 1973) and from work on this particular group by Herzing (1993b, 1994). It is possible, and quite probable, that their whistles contain individual characteristics. I am inclined to believe, based upon the literature and a few anecdotal observations of this group of spotted dolphins, that spotted dolphins do at times emit individually distinct or signature whistles (Caldwell *et al.*, 1973; Herzing, 1994).

Distinct whistles might be produced in a more limited context as compared with their broad context suggested by the signature whistle hypothesis (SWH, Caldwell *et al.*, 1990). Briefly, the SWH states that dolphins have signature whistles that they use primarily to broadcast identity to conspecifics. Smolker *et al.* (1993) present evidence suggesting that bottlenose dolphins in Shark Bay, Australia, use signature whistles as contact calls just prior to initiating a reunion with conspecifics. Their study focused on mother/calf pairs, with anecdotal reports of older individuals. Their observations, made during focal follows of separated bottlenose dolphin mother/calf pairs, documented that the calf produced a signature whistle just prior to rejoining its mother (Smolker *et al.*, 1993).

Specific maternal vocalizations have been reported in captive and free-ranging bottlenose dolphins (e.g., McCowan & Reiss 1995b, Smolker *et al.*, 1993, respectively). The applicability and usefulness of the recognition of auditory cues between mother/calf pairs has also been extensively reported in seals, sea cows, and ungulates (e.g., Insley, 1992; Barfield *et al.*, 1994). Contact calls used during mother/pup separations have been documented in pinniped species (Insley, 1992); and species-specific cues have been noted in different species sharing overlapping ranges (Insley, 1992).

Other support for the primary use of signature whistles as contact calls can be gleaned from the review by Caldwell *et al.* (1990) and from work done on the whistling behavior of bottlenose dolphins in Sarasota Bay, Florida (Sayigh *et al.*, 1990; Sayigh, 1992; Sayigh *et al.*, 1995). In most cases, individuals' vocalizations were recorded while separated from conspecifics. In all cases, individual dolphins produced stereotyped calls that were labeled signature. It is possible that the stereotyped call could be indicative of stress; however, at least for the Sarasota Bay dolphins, individuals did not show behavioral, postural or hormonal signs of stress (Wells *et al.*, 1987). The production of repetitive whistle contour patterns in these contexts could also be explained by the interpretation of signature whistles as contact calls, as defined by Smolker *et al.* (1993).

BUBBLE EMISSIONS - OBSERVATIONS OF PRODUCTION

This encounter provides a good example of the alternating bouts of vocal behavior in the social activities of spotted dolphins. At the most basic level, it indicates that not all interactions are affiliative among individuals living in groups. At times, there is competition and conflict. Vocal signal exchanges provide clues to not only the activity occurring but also give insight into the potential motivations and internal referents of the interacting individuals (Smith, 1965; Dusenbery, 1992). Thus, when the spotted dolphins in this encounter were engaged in ramming and raking and jaw clapping exchanges and displays, they also were emitting squawks and intense, rather monotonic whistles (long duration, type #9). Bubble streams, trails, and clouds were coupled with vocal emissions from several individuals (although ascribing specific vocal patterns to individuals was not possible

due to the level of activity and close proximity of the dolphins): these bubbles could be indicators of the level of excitement - more bubbles were produced during the aggressive exchanges compared with the affiliative behaviors. Or they could be a means for individual dolphins to obscure themselves as was described for humpback whales (Silber, 1986). When dolphins were exchanging hits and chasing each other, they also emitted many intense whistles, all coupled with bubble streams. It was difficult for observers to follow specific individuals visually and certainly vocally, which could be a potential goal of bubble emissions during aggressive interactions.

Bubble releases may have different functions depending on the behavioral activity in which they are produced or even depending on the type of air pocket released. For example, it is possible that dolphins use some types of bubbles, such as bubble clouds, defensively to diffuse the energy content of directed, high energy vocalizations from conspecifics during aggressive social contexts. Bubbles can act as barriers to deflect energy from different sources (Sharpe & Dill, 1993). In fact, humpback whales have been observed to use bubble rings and lines to corral fish during foraging contexts (Sharpe & Dill 1993). Use of such a defensive posture (or bubble release) is supported by evidence that some dolphins can produce loud impulse sounds that have been postulated to be used in foraging (Norris *et al.*, 1985; Marten *et al.*, 1988). If the dolphins are capable of stunning prey with these loud impulse sounds (similar to squawks, but not specifically the 'bang' noise), then they are probably capable of using them on conspecifics during fighting. Thus, while dolphins may have developed a technique to use specific sounds aggressively, it makes sense evolutionarily that they have developed a tactic to countermand the offensive maneuvers of conspecifics.

Another variation on the function of bubble streams comes from young spotters producing screams. Screams were only produced by calves and juveniles and were usually accompanied by a bubble stream. The "leaky" or raspy sound of a scream may indicate early development, and therefore lack of experienced vocal control in young individuals. Vocal learning in whistle production has been demonstrated in bottlenose dolphins (Tyack, 1986b; Sayigh *et al.*, 1990; McCowan & Reiss, 1995c). It has also been suggested that bottlenose dolphins must learn the correct context for specific tones. An example of vocal learning of an auditory cue for use in a specific context is

that of the distinct alarm calls of vervet monkeys (Seyfarth *et al.*, 1980). It is possible that spotted dolphins also learn different vocalizations, but screams could also be explained by internal motivations: the screaming dolphin is involved in heightened play with other dolphins and gets "carried away". More data are warranted to either examine the possibility of vocal learning in this free-ranging dolphin group.