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Vocalizations and associated underwater behavior of free-ranging Atlantic spotted dolphins, *Stenella frontalis* and bottlenose dolphins, *Tursiops truncatus*

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Abstract

Atlantic spotted dolphins, *Stenella frontalis*, and bottlenose dolphins, *Tursiops truncatus*, were observed underwater from 1985–1994. Simultaneous vocalizations and behavior were recorded using an underwater video with direct hydrophone input. Individual dolphins within this community were monitored, sexed, and observed for ten summer field seasons. Ten types of vocalizations were associated with underwater behaviors, and in some cases individual dolphins. This paper describes the contextual/social use of the signature whistle, excitement vocalization, genital buzz, squawk, synchronized squawk, scream, and bark. Razor buzzes, trills, and upswept whistles were associated with foraging and feeding behavior.

Although many of these vocalizations have been described in the literature, their association, described here, with specific underwater behaviors and age class information provides additional contextual information about their potential use as communication signals. This paper provides a descriptive field guide to the natural history and behavior of Atlantic spotted dolphins in the Bahamas including specific communication signals and concurrent behavioral activity.

Introduction

It has long been thought that dolphin communication is both complex and contextual (Johnson, 1993; Tavolga, 1983). Sources of information, other than the acoustic signal itself, are important in the definition of context and communication for other species, specifically birds and mammals, including audience effect, the history of the animal, and individual differences (Smith, 1977). But because of the highly developed acoustic sense in dolphins, researchers have emphasized the recording and analysis of vocalizations (Evans, 1966; Herman & Tavolga, 1980; Norris, 1969; Popper, 1980; Watkins & Wartzok, 1985).

Dolphins communicate using both vocal and non-vocal signals (Wursig *et al.*, 1990). Qualitative descriptions of behavior and associated vocalizations were first reported for captive dolphins (Caldwell & Caldwell, 1968; McBride & Hebb, 1948; Puente & Dewbury, 1976; Tavolga & Essapian, 1957). More recently quantitative measures have been used in studies of free-ranging delphinids including spinner dolphins, *Stenella longirostris* (Driscoll & Ostman, 1991; Norris *et al.*, 1994), pantropical spotted dolphins, *Stenella attenuata* (Pryor & Shallenberger-Kang, 1991), killer whales, *Orcinus orca* (Simula & Ugarte, 1993), hectors dolphins, *Cephalorhynchus hectori* (Slooten, 1994), and the bottlenose dolphin, *Tursiops truncatus* (Connor *et al.*, 1992; dos Santos *et al.*, 1990; Schultz *et al.*, 1995; Smolker *et al.*, 1993). Nevertheless, underwater behavioral observations and associated vocalizations of free-ranging dolphins remain sporadic.

Associating vocalizations with the underwater behavior of dolphins has proved difficult due to the lack of underwater access to animals and life history, sex, and relationship information. Limited reports on the behavior and vocalizations of Atlantic spotted dolphins, *Stenella frontalis* (formerly *S. plagiodon*), have been made (Caldwell & Caldwell, 1966, 1971; Caldwell *et al.*, 1973; Herzing, 1991, 1994; Wood, 1953). This paper describes underwater behavior and associated vocalizations used during social interaction and foraging behavior of free-ranging Atlantic spotted dolphins and bottlenose dolphins. It is meant to be a descriptive field guide to natural behavior, both vocal and non-vocal, for dolphins in the wild.

Methodology

Since the mid 1970s, a community of habituated Atlantic spotted dolphins in the Bahamas have been

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Table 1. Incidences of behavioral contexts observed

	Mother/calf Alloparental	Courtship	Discipline	Aggression		Sexual play	Foraging/Feeding	
				intra	inter		intra	inter
1985	4	—	—	—	—	—	2	—
1986	3	—	—	—	2	—	5	—
1987	4	3	1	2	2	2	11	—
1988	4	4	2	—	2	1	4	—
1989	4	6	1	1	2	1	9	—
1990	8	2	1	—	1	2	11	—
1991	8	10	2	1	4	4	8	—
1992	12	6	1	5	5	1	4	2
1993	21	13	10	2	8	7	8	—
1994	13	18	14	4	6	7	3	1
Totals	81	62	32	15	32	25	65	3

accessible to underwater observation (Brynes *et al.*, 1989; Herzing, 1989, 1993). This community of dolphins inhabit an offshore, shallow sandbank and its adjacent deep waters off Grand Bahama Island in the Bahamas. The Bahama Islands are an archipelago in the tropical West Atlantic southeast of Florida. Surrounded by deep water and the Florida straits, the shallow water Bahamas banks are thick, submerged platforms of calcareous rocks, the remains of ancient reefs. Many different habitats are present including fringe and patch reefs, atolls, grassy flats, and ledges.

One hundred and fifty-five individual spotted dolphins were identified by photographs and video of dorsal fins, flukes and constellations of spots. These dolphins were sexed via direct observation of the genital area, and categorized into age classes of their degree of spotting and color phase, and repeatedly observed over the ten year period (Herzing, in press). Thirty bottlenose dolphins were individually identified and sexed when they interacted with spotted dolphins using similar methods.

Underwater behavioral and sound data were recorded using underwater video cameras with audio channels flat to 22 kHz (Sony CCDV9 8 mm, Yashica KV 1 Hi 8 mm) with direct Labcore 76 hydrophone (frequency to 20 kHz, -192 dB re 1 *u* Pa) into the underwater housing to assure simultaneous recordings of underwater behavior and vocalizations. Vocalizations were processed using a Spectral Innovations 32-bit floating point digital signal processor with a 125kHz 16 bit analog to digital card (maximum sample rate of 62.50 kHz) and stored on a Macintosh 11ci computer. Measurements of the digitized vocalizations were then measured using Canary 1.1 acoustic measurement software. Identification of a vocalizing dolphin was made when visible bubble emissions were synchronized with a vocalization and when the

Table 2. Incidences of vocalization type observed

	Signature whistle	Excitement vocalization	Genital buzz	Squawk	Synchronized squawk	Scream	Bark	Razor buzz
1985	2	—	—	1	—	—	—	1
1986	1	—	1	1	—	—	—	1
1987	1	16	1	6	—	—	—	4
1988	—	4	—	3	—	—	—	1
1989	1	21	2	2	—	—	—	2
1990	20	21	4	6	—	—	—	3
1991	30	15	7	8	—	—	—	7
1992	26	13	17	2	1	4	2	6
1993	62	19	13	9	1	1	—	7
1994	34	12	5	8	—	2	2	9
Totals	177	121	50	46	2	7	4	41

Table 3. Vocalizations and associated underwater behavior (*Stenella frontalis/Tursiops truncatus*)

Vocalization type	Spectral description	Behavioral context	Species, age class and sex
Signature whistle	Frequency modulated (FM) whistle 4–18 kHz 0.5–8 s Bubbles emitted from blowhole occasionally	Mother/calf reunions	Spotted dolphins All age classes Female/male offspring
		Alloparental care	Spotted dolphins Juvenile, young and old adults Females/males
		Courtship	Spotted dolphins Females/males
Excitement vocalization	Burst-pulsed vocalization with overlapping signature whistle 4–18 kHz 2–30 s duration Bubbles emitted from blowhole	Distress or excitement	Spotted dolphins All age classes Most frequently calves Females/Males
Genital buzz	High repetition-rate clicks 1.2 kHz–2.5 kHz 8–2000 clicks/s 6–20 s duration	Courtship	Spotted dolphins Juvenile, young, and old adults Males
		Discipline	Intra and interspecific Adult, juveniles Females/males
Squawk	Broad-band burst-pulsed vocalization 0.2–12 kHz 0.2–1.0 s duration 200–1200 clicks/s	Agonistic and aggressive	Intra and interspecific All age classes Females/males
		Sexual play	Intra and interspecific All age classes Females/males
Scream	Overlapping FM whistles 5.8–9.4 kHz 2.5–4.0 s duration	Agonistic and aggressive	Intra and interspecific Juvenile, young and old adults Males
Bark	Burst-pulsed vocalization 0.2–2.0 kHz 0.5–1.0 s duration	Agonistic and aggressive	Intra and interspecific Juvenile, young and old adults Males
Synchronized squawks	Burst-pulsed vocalization 0.1–15 kHz Main energy 0.1–2.2 kHz 0.9–1.0 s duration	Agonistic and aggressive	Intra and interspecific Juvenile, young and old adults Males

dolphin was alone or in close proximity to the recording unit.

Ad lib and focal sampling were used during this study (Altmann, 1974). Associations of vocalizations were made with general categories of behavior including: (1) Foraging/Feeding: dolphins searched for or consumed prey items, (2) Agonistic/Aggressive: threatening or intensely dominating behavior displayed towards another dolphin(s), (3) Affiliative/Social: socially oriented behavior not sexual, agonistic, submissive, or aggressive in nature. Included intradolphin tactile behavior and object play, (4) Sexual Play: non-mating genital contact or orientation, (5) Courtship: focal dolphin(s) were engaged in foreplay and pursuit, which culminated in mating or attempted mating. Sex of the individual dolphins were known, (6) Parental: mother interacted with or supervised calf. Included nursing and general mother/calf behavior, (7) Alloparental: supervising dolphin interacted with or tended younger dolphin, where the relationship of focal dolphin(s) were known, (8) Disciplinary: focal dolphin(s) interacted with and reprimanded other dolphin(s), which included punishment or reestablishment of order, (9) Distress/Excitement: focal dolphin(s) erratically swam and vocalized.

Intraspecific behavior refers to spotted dolphins unless specified otherwise. Behaviors involving both

Table 4. Foraging/feeding vocalizations (*Stenella frontalis*/*Tursiops truncatus*)

Vocalization type	Spectral description	Behavioral context	Species, sex and age
Razor buzz	Echolocation click train 2.0–6.0 kHz 200 clicks/s Sustained for minutes Aural quality is similar to an electric razor	Foraging/feeding Individual or group spread formation on bottom, horizontally scanning along bottom	Intra and inter-specific All ages Females/males
Echolocation with rostrum in sand	Echolocation click train 2.0–6.0 kHz 400–500 clicks/s Short, 2–3 s durations	Foraging/feeding Individual has rostrum buried in sand	Intra and inter-specific All ages Females/males
Echolocation with overlapping trills and upswept whistles	Echolocation click train 2.0–6.0 kHz 8–100 clicks/s Trills repetitive, below 5.0 kHz Whistles 4.8–16 kHz	Foraging/feeding Ledge and reef exploration and foraging	Bottlenose dolphins All ages Females/males

species were categorized as interspecific activity. Behavioral contexts do not refer to a specific behavioral unit of action, as in an ethogram, but instead indicate the behavioral setting, or social situation or action of a focal dolphin or focal group of dolphins. The function of specific behaviors should not be considered final or conclusive since developmental and other contextual aspects need to be analyzed for more complete understanding of this communication system.

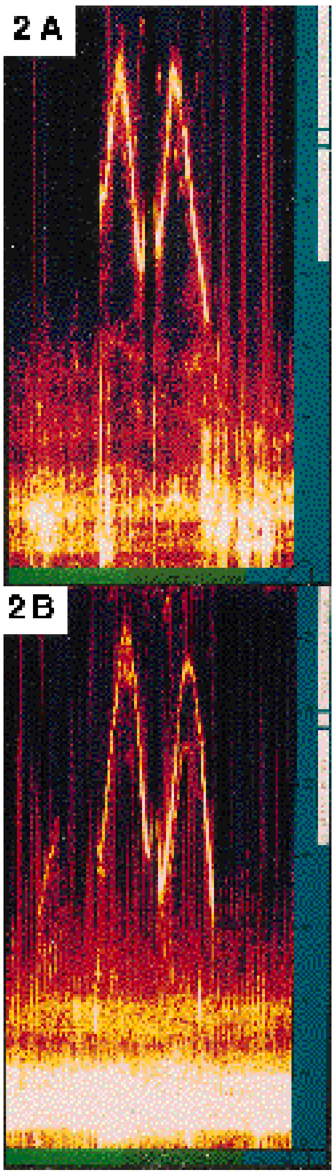
Results

A variety of behavioral contexts were observed over the years and are summarized in Table 1. The occurrence of specific vocalization types is also summarized in Table 2. All vocalization types, their spectral descriptions, and behavioral contexts are presented in Tables 3 and 4.

Vocalization types

Whistles/signature whistles. Whistles were the easiest vocalization to measure and associate with an individual spotted dolphin since bubbles were often expelled from the blowhole during this vocalization and at close proximity to the video camera (Fig. 1). One hundred and forty-six whistles were associated with thirty-three specific individual spotted dolphins of varying age classes including thirteen males and twenty females. Examples of a range of ages and sexes, including five mother/calf pairs, three maturing females, and four maturing males with their associated whistles are given (Figs 2–8). Individual dolphins produced, among other whistle types, a predominate and unique repetitive whistle that was consistently observed up to ten years for some dolphins. Therefore, for this report, whistles that were recorded repeatedly from individuals were considered signature whistles as defined by the criteria for other species (Caldwell *et al.*, 1990). Whistles ranged between 4 and 18 kHz, and varied in duration from 0.5 to 8 s.

Figure 1. Bubbles are expelled from the blowhole as an individually identifiable dolphin whistles.



Figures 2–8. Spectrograms of signature whistles for individual dolphins of varying age class and sex. Many of the listed individuals have whistles that have been visually scanned, over ten years, for consistency but have not been captured electronically. Therefore, a minimum number (n) of captured whistles, and repetitive years (yrs) during which whistles were recorded are given. Frequency is on the vertical and time on the horizontal axis for all figures.

Figure 2. Signature whistles of mother/calf. (a) Nippy—young adult female (n=4, yrs=2); (b) Nassau—3-yr-old female calf (n=11, yrs=3).

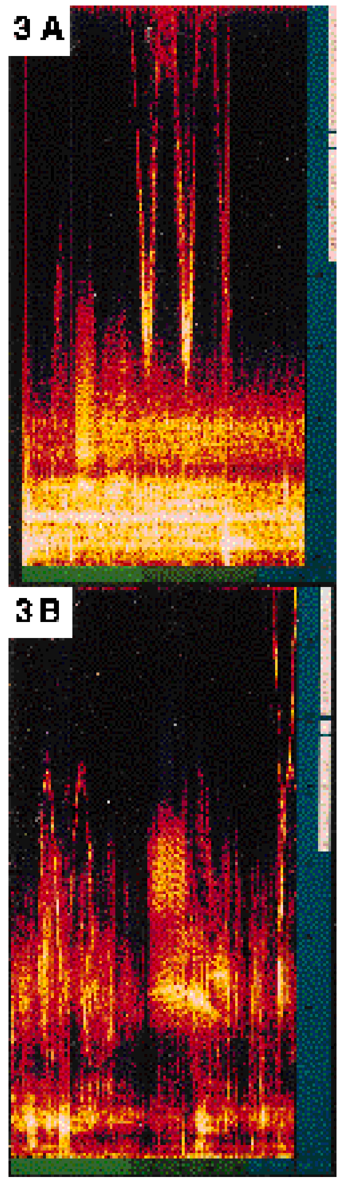


Figure 3. Signature whistles of mother/calf. (a) LGash—young adult female (n=6, yrs=3); (b) LHali—newborn female calf (n=2, yrs=1).

Signature whistles were observed in three behavioral contexts:

1. Mother/calf reunions. Mothers produced their own signature whistle after calves departed from them. After the mother whistled, the calves rejoined her.

2. Alloparental care. Older conspecifics, including male and female dolphins, in association with younger dolphins, produced their own signature whistles prior to the retrieval of younger dolphins.

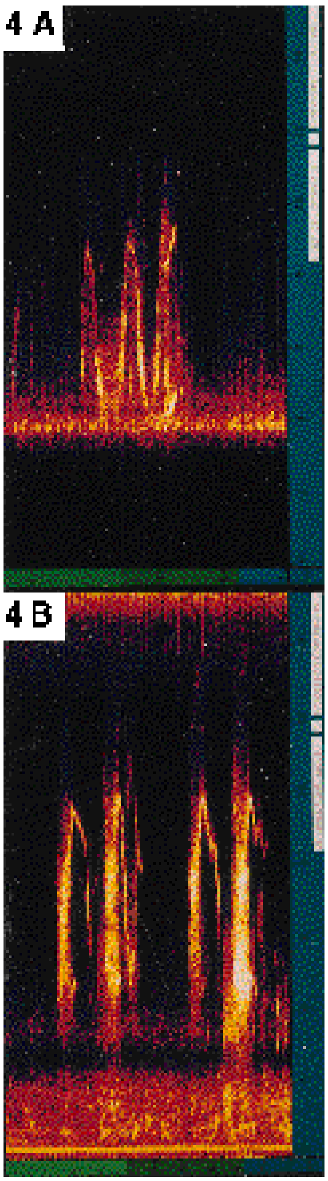


Figure 4. Signature whistles of mother/calf. (a) Mugsy—young adult female (n=1, yrs=1); (b) Mel—2-yr-old male calf (n=1, yrs=1).

Tail-slapping (right side up or inverted) on the surface of the supervising dolphin was also involved in successful retrieval.

3. Courtship. Female and male spotted dolphins were observed repetitively broadcasting their own signature whistle during attempted courtship and mating activity. Male coalitions, as described by de Waal & Harcourt (1992), of three to four spotted dolphins chased and surrounded a female and eventually mated with her.

Excitement vocalization
A variation on the signature whistle was the excitement vocalization (Fig. 9). This vocalization was a combination burst-pulsed sound (in the lower 4–8 kHz range) and signature whistle of the vocalizer (8–18 kHz). The duration of this vocalization ranged from 2.0–30 s. During the production of this vocalization, dolphins were highly erratic in their swimming behavior and emitted a stream of bubbles.

The excitement vocalization was observed in only one behavioral context:

Distress/Excitement. Excitement vocalizations were observed during periods of excitement or distress, frequently by a calf under three years of age. The trigger for distress behavior varied from intraspecific social behavior to the presence of human observers in the water. After the production of the excitement vocalization began, an older dolphin was observed to calm the youngster down by a slight pectoral flipper brush on the flank of the vocalizing calf. Duration of this vocalization rarely exceeded 30 s before a conspecific was successful in calming the vocalizer down.

Genital buzz
The genital buzz was a low frequency, high repetition rate echolocation train directed towards the genital or mid-section of a conspecific (Figs 10a and 10b). This vocalization ranged from 1.2–2.5 kHz with durations up to 20 s. Repetition rates of 8 clicks/s up to 2000 clicks/s were recorded (Fig. 10c).

This vocalization was observed in two behavioral contexts:

Courtship. The sequence of courtship included genital inspection and 'buzzing' by the male who assumed an exaggerated S-posture as he approached the female from beneath. In later stages of courtship the male inverted and approached from underneath the female, ending in copulation. Bubble clouds were expelled by young adult males during this behavior. Attempts at courtship by immature males were often unsuccessful and escalated into aggressive sequences (see below).

In one instance, an adult male buzzed a male calf in the genital area and then copulated with the calf. The adult male then copulated with the calf's mother, followed by the calf who copulated with its mother. This observed sequence may have been an example of observational learning, since the vocal and non-vocal signals used were similar to adult courtship behavior, although it is difficult to

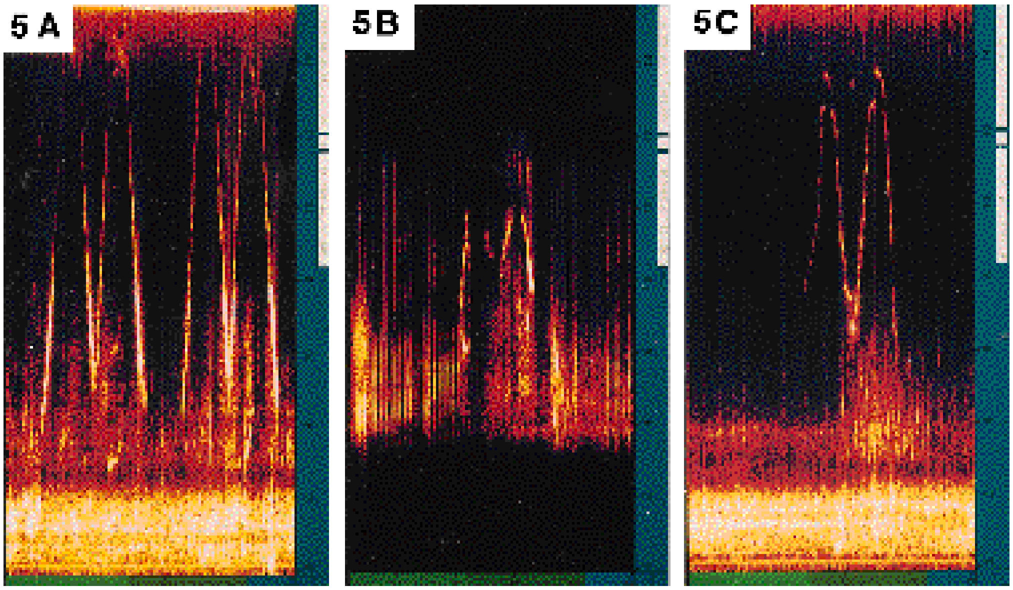


Figure 5. Signature whistles of mother/two calves. (a) Luna—old adult female (n=14, yrs=3); (b) Diamond—4-yr-old female calf (n=2, yrs=1); (c) Latitude—3-yr-old male calf (n=9, yrs=2).

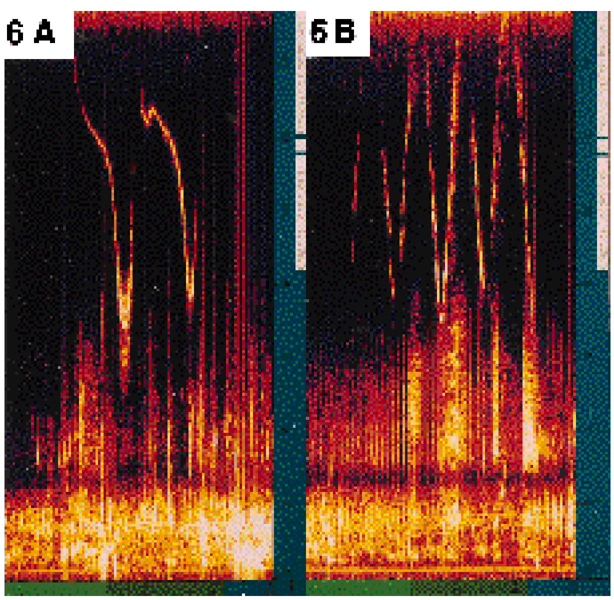


Figure 6. Signature whistles of juvenile females. (a) Trimy—juvenile female (n=1, yrs=1); (b) Katy—juvenile female (n=9, yrs=3).

observe the complete developmental process of free-ranging dolphins.

Discipline. When mothers were unsuccessful in retrieving their calves they swam inverted and buzzed the genital area of their offspring. Mothers eventually made physical contact with their rostra to the calf's flank. Extreme disciplinary sequences, where a mother physically held the calf down on the sandy bottom, were also observed.

Groups of five or more dolphins were observed in tight physical contact, with their rostra pointed

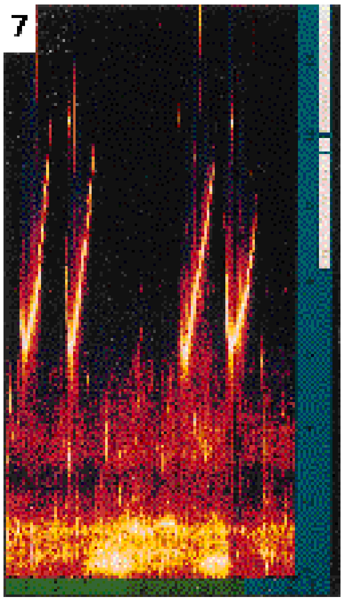


Figure 7. Signature whistle of young adult female. WhitePatches—young adult female (n=13, yrs=3).

towards, but not touching, another dolphin, while they buzzed the genital area of the individual, who initially tried to swim away from the group. When physical contact of their rostra to the individual's body was finally made, the single dolphin became passive and allowed itself to be pushed around by the group. In some instances, the single dolphin was held down to the bottom, similar to disciplinary actions between a mother and calf. This behavioral sequence was observed both intraspecifically within and between all age classes of spotted dolphins, and interspecifically between juvenile and young adult spotted and bottlenose dolphins.

Squawks

Squawks were recorded during bouts of agonistic and aggressive behavior and during sexual play. Components of this behavior included head-to-head orientations (Fig. 11a), figure-eight circling motions, body charges, and open-mouth behavior (Fig. 11b). Squawks are broad-band, burst-pulsed sounds, and were observed during intra- and interspecific behaviors. Squawks ranged in frequency from 0.2–12 kHz although the main energy was found in the lower frequencies of 1.1–2.4 kHz (Fig. 11c). Duration ranged from 0.2–1.0 s. Repetition rate varied from 200 click/s to 1200 click/s.

Squawks were recorded in four behavioral contexts:

Agonistic/Aggressive–Intraspecific. Threats and postures between spotted dolphins consisted of head-to-head displays, open-mouth postures, body charges, and tail-slaps to the head. Aggression was frequently observed between male groups, and between unreceptive/unapproachable females and courting males. In male groups, torus bubbles (bubble rings) were also observed.

Agonistic/Aggressive–Interspecific. The most highly escalated aggression was observed between spotted and bottlenose dolphins. Groups of spotted male dolphins faced off with solitary or small groups of bottlenose dolphins and chased them as a solidified group (see synchronized squawks). Rapid head movements and occasional jaw claps were also observed in this context.

Sexual Play–Intraspecific. Squawks were recorded during various types of sexual play between spotted dolphins. This behavior took the form of reciprocal tactile stimulation between mothers and calves, juveniles, courting males and females, and adult females and males.

Sexual Play/Courtship–Interspecific. Interspecific sexual play was observed between bottlenose and spotted dolphins. This included adult male bottlenose dolphins who copulated with young female spotted dolphins, adult female bottlenose dolphins who solicited copulation from young male spotted dolphins, and male bottlenose dolphins who rubbed genitalia, side-mounted, and copulated with male spotted dolphins (Figs 12a and 12b).

Screams

Screams were also associated with intraspecific and interspecific agonistic/aggressive behavior. The scream consisted of overlapping frequency-modulated whistles that ranged from 5.8–9.4 kHz and lasted 2.5–4.0 s (Fig. 12c).

Screams were recorded in two behavioral contexts:

Agonistic/Aggressive–Intraspecific. The scream was observed only during escalated agonistic/aggressive contexts in groups of ten or more male spotted dolphins. Other signals included those described above for agonistic and aggressive sequences.

Agonistic/Aggressive–Interspecific. The scream was also observed during highly escalated agonistic/aggressive behavior between male dolphins of both species during interspecific conflict.

Barks

Barks were recorded during the same highly escalated agonistic/aggressive behavioral sequences described above for screams. Barks were a low-frequency, burst-pulsed vocalization that ranged

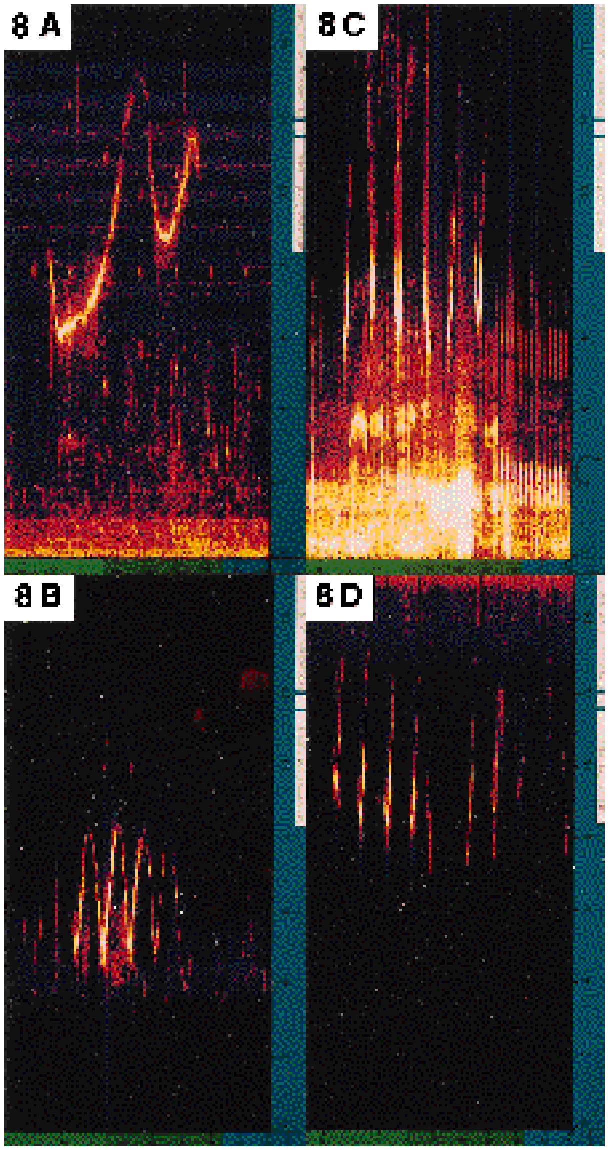


Figure 8. Signature whistles of young adult males. (a) Stubby—young adult male (n=6, yrs=1); (b) Punchy—young adult male (n=1, yrs=1); (c) Knuckles—young adult male (n=1, yrs=1); (d) Scquew—young adult male (n=1, yrs=1).

from 0.2–2.0 kHz and lasted from 0.5–1.0 s (Fig. 12d).

Synchronized squawks

In highly escalated aggressive activity, male spotted dolphins coordinated their swimming behavior and postures during synchronized series of squawks (Fig. 13a). Synchronized squawks were a highly coordinated burst-pulsed vocalization that ranged in frequency from 0.1–15 kHz, with main energy from 0.1–2.2 kHz, and durations from 0.9–1.0 s (Fig. 13b). Young males showed partial synchronization of swimming behavior and squawks (Fig. 13c) but were not fully coordinated in their efforts.

Synchronized squawks were recorded in two behavioral contexts:

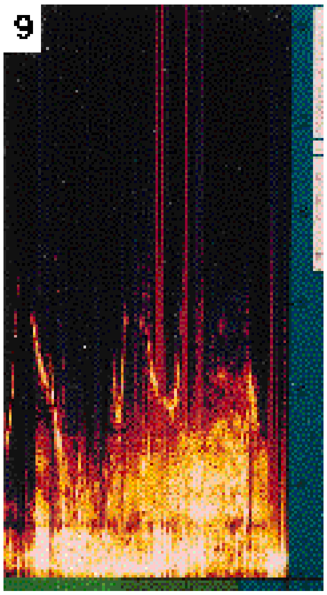


Figure 9. Spectrograms of an excitement vocalization of juvenile dolphin.

Agonistic/Aggressive–Intraspecific. During fights with other male groups, male spotted dolphins synchronized their inverted swimming and breathing within touching proximity of each other, while squawking.

Agonistic/Aggressive–Interspecific. Male spotted dolphins also displayed synchronized behavior during escalated fights with bottlenose dolphins. When multiple bottlenose dolphins singled out a spotted male dolphin, the spotted dolphin floated passively while being mounted by the bottlenose, which often included penile intromission. When additional male spotted dolphins arrived and got involved, the spotted dolphins synchronized their swimming movements and vocalizations and chased the male bottlenose dolphins out of the area. Young male spotted dolphins demonstrated similar behavior but were usually uncoordinated in their synchronization. In these cases, older male spotted dolphins intervened and assisted the younger males and chased the bottlenose away.

Razor buzz, trill and upswept whistle

Atlantic spotted dolphins and bottlenose dolphins echolocated while scanning and digging for buried prey in sandy bottoms. Vocalizations were recorded during two behavioral contexts:

Foraging/Feeding–Intraspecific—bottlenose dolphins. Bottlenose dolphins were often associated with nurse sharks, *Ginglymostoma cirratum*, while they scanned the bottom (Fig. 14a). Two distinct techniques for searching for prey under the sand were observed. (1) Bottlenose dolphins spread out and swam less than 1 m above the bottom, scanning along their longitudinal axis, side to side, while swimming forward and paralleling the bottom sediment; (2) bottlenose dolphins alternated clockwise and counterclockwise scanning on their longitudinal axis, 3 or more meters above the bottom, in the water column, pointing at an angle or vertically down. Upon descending they would further explore

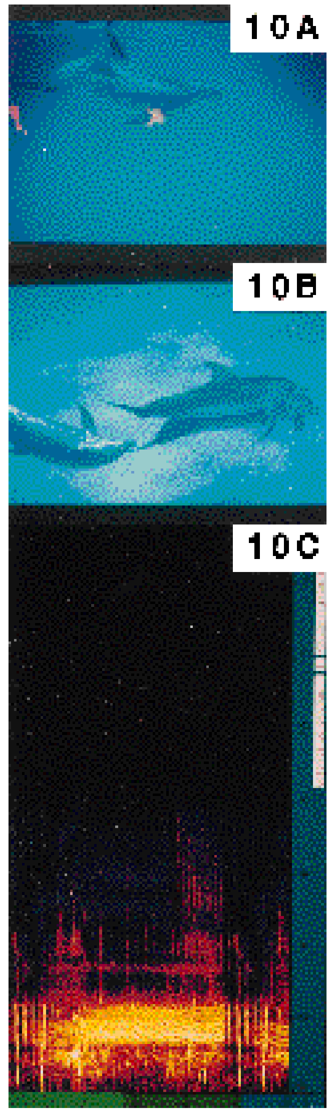


Figure 10. Courtship behavior. (a) An S posture by an adult male; (b) a male, in an inverted posture, orients on and chases a female; (c) spectrogram of a genital buzz.

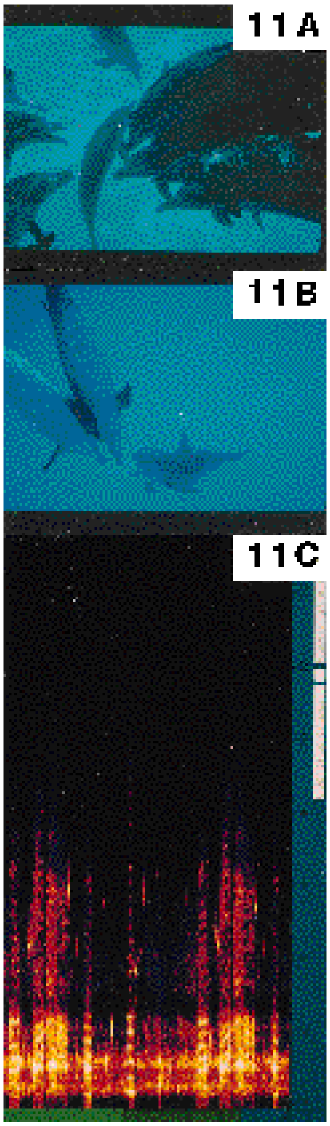


Figure 11. Aggressive behavior. (a) A group head-to-head stance; (b) a female in head-to-head and open-mouth stance towards two males; (c) spectrogram of multiple squawks.

the bottom with echolocation, using circular scanning motion and jaw claps. Both these techniques were observed to be successful for targeting a prey item.

The razor buzz (aurally distinguishable from other echolocation click trains by the intensity and 'tinny' quality) ranged from 2.0–6.0 kHz with repetition rates up to 200 clicks/s (Fig. 14b). In the latter stages of digging, bottlenose dolphins oriented vertically with their rostra in the sand (Figs 15a and 15b). During this time, echolocation rates increased to 400–500 clicks/s when rostra were submerged in the sand (Fig. 15c).

Bottlenose dolphins also used the razor buzz in conjunction with trills (repetitive series of discrete beeps below 5.0 kHz) and upswept whistles (ranged from 4.8–16.0 kHz) during 'ledge' feeding (Fig. 16). In June 1990, a group of 20 bottlenose dolphins were observed for 2 h foraging on a coral reef in 3 m of water. Bottlenose dolphins explored under ledges and in squirrel fish holes (possible prey items included family *Pomadasyidae*, *Lutjanidae*, and *Holocentridae*). Two nurse sharks also foraged under the same ledges.

Foraging/Feeding–Intra and Interspecific. Spotted dolphins were observed intraspecifically foraging, using general echolocation click trains, on the sandy bottom. Prey items included flounder (family *Bothidae*), lizardfish (family *Synodontidae*), wrass (family *Labridae*), blenny (family *Tripterygiidae*), clinid (family *Clinidae*) and conger (family *Congridae*). Interspecifically, on two sequential days in 1991, 30 spotted dolphins and 2 bottlenose dolphins were observed foraging together on a concentrated patch of loose sand, approximately 20 m × 20 m (Fig. 17a). This event was unusual because of the density of foraging dolphins in a small area of bottom. Echolocation clicks were directed into the sand by dolphins at the rate of 400–500 clicks/s (Fig. 17b). Bottomfish appeared to be disoriented or stunned as they emerged from the sand and became easy prey for the dolphins. Some fish were so stunned that we collected them, by hand, for specimen samples as they floated along the bottom. The little tunny, *Euthynnus alletteratus*, associated with foraging spotted dolphins and were observed taking fish that the dolphins ignored or lost in the hunt.

Discussion

Whistles

Whistles display relatively low directionality but may function as long-distance social communicative signals due to their highly localizable frequency modulated characteristics (Norris & Dohl, 1980). Associations between whistles and behavior include increased whistling rate during excitement and stress in the Hawaiian spinner dolphin (Norris *et al*., 1994), during bow riding and feeding in the common dolphin, *Delphinus delphis* (Busnel & Dziedzic, 1966), during feeding in the pilot whale, *Globicephala* sp. (Dreher & Evans, 1964), during fleeing and cooperative behavior (Evans, 1966) and during mother/infant reunions in bottlenose dolphins (Smolker *et al*., 1993).

Caldwell & Caldwell (1965) first suggested, and later revised (Caldwell *et al*., 1990), that repetitive

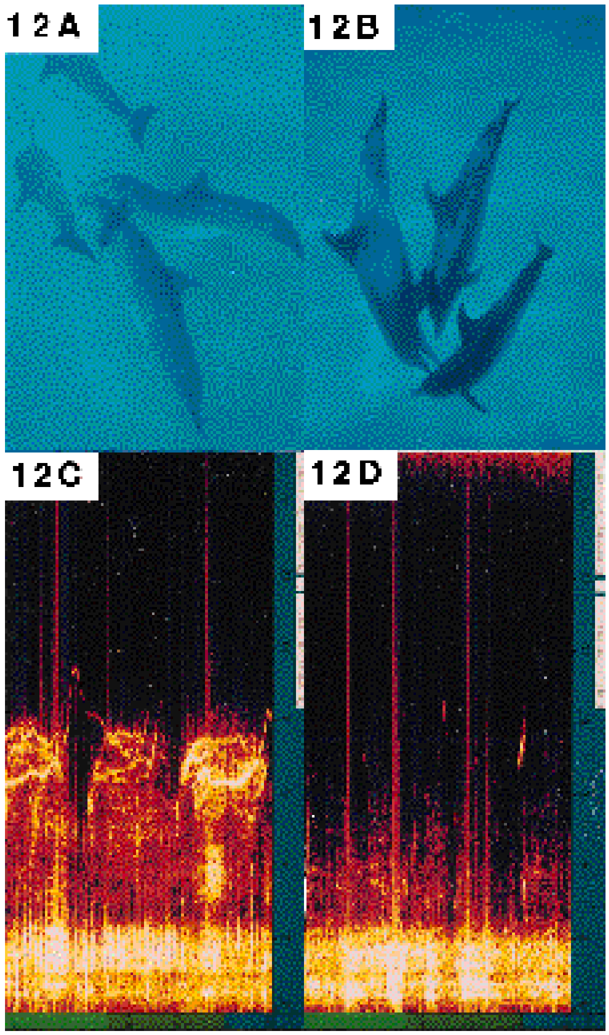


Figure 12. Interspecies sexual play/aggression. (a) Two male bottlenose dolphins, with erections, chasing two male spotted dolphins; (b) male bottlenose dolphin open-mouth on male spotted dolphins; (c) spectrogram of multiple screams; (d) spectrogram of low-frequency barks.

whistles, termed 'signature' whistles, may be individually specific and may function as identifiers of individual dolphins. Signature whistles have already been described for the Atlantic spotted dolphin (Caldwell *et al*., 1973). Recently, an expansion/replacement theory termed 'whistle repertoire' theory, which normalizes all whistles to their common features and which acknowledges the potentially contextually appropriate social situations for whistle use, has recently been proposed (McCowan & Reiss, 1995). Although some individual Atlantic spotted dolphins have a unique and predominate distinctive whistle, new quantification and normalization techniques described above have not yet been applied to these data. The existence and stability of 'signature' whistles, as described by Sayligh *et al*. (1990), should not discount the possibility that other uses of these whistles exist. Analysis of the full repertoire and contextual use of vocalizations in the wild should eventually yield a functional description of these communication signals.

The use of bubble streams as identifiers of both the individual vocalizing and, as representative of the full repertoire of whistles, has been verified by

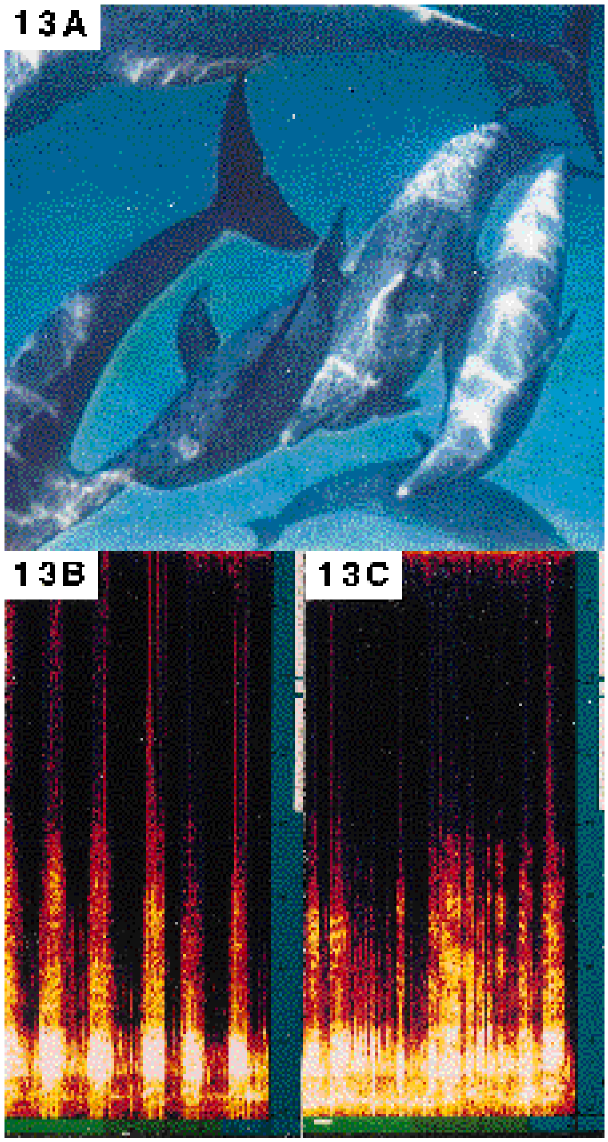


Figure 13. Interspecies aggression. (a) Young adult male spotted dolphins inverted and chasing a male bottlenose dolphin; (b) spectrogram of a series of synchronized squawks; (c) spectrogram of a series of squawks produced by juvenile male spotted dolphins during attempted synchronization of swimming behavior.

other researchers (McCowan & Reiss, 1995). Although more technologically sophisticated techniques for identifying vocalizing dolphins have been attempted in the wild (Dudzinski *et al*., 1995), they proved unsuccessful for discerning vocalizing individuals in large, close-proximity groups of interacting dolphins. The need for techniques to identifying vocalizing individuals remains to be explored in the future.

An example of the developmental and contextual complexity of categorizing whistles is the excitement vocalization described. This vocalization is similar to the 'whistle-squawk' described by Caldwell & Caldwell (1967) who reported that

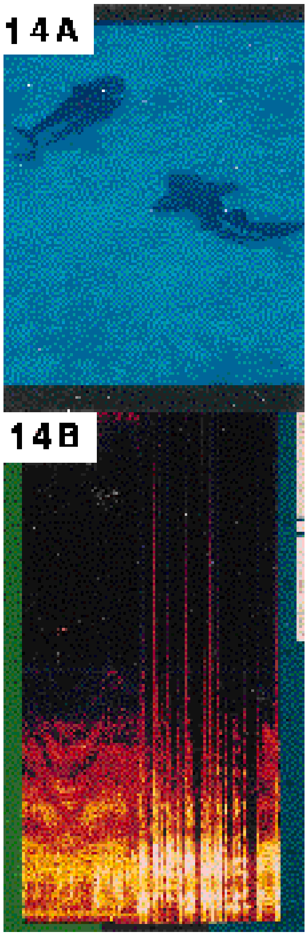


Figure 14. Foraging behavior—bottlenose dolphins. (a) Bottlenose dolphin foraging in proximity to a nurse shark; (b) spectrogram of razor buzz during scanning. (Clicks appear harmonic in nature due to the high repetition rate of >200 clicks per second [Watkins, 1967].)

bottlenose dolphins, when removed from the water emitted this vocalization. They suggested that this type of sound is emitted when the animal is 'protesting' and also reported a dominant male who never whistled without squawking simultaneously in a variety of behavioral contexts. This may indicate that dolphins emit this sound when they are distressed, excited, or have lost control of their vocalization apparatus during the production of this type of combined sound. Reiss (1988) also reported the presence of 'whistle squawk' for two infant bottlenose dolphins, and suggested that these sounds are produced during more emotional contexts of behavior.

Genital buzz
Although the genital buzz described for Atlantic spotted dolphins is not found in the literature, echolocation trains termed a 'buzz' have been reported in threat situations (Lilly & Miller, 1961), and during general social interactions (Reiss, 1988). The highest intensities and frequencies of echolocation clicks emanate forward from the melon in a cone of directional sound (Au *et al.*, 1978; Norris *et al.*, 1961). Although echolocation has been associated with the gathering of environmental information and navigation, the intense level of energy emission has recently been the topic of discussion in functional aspects of cetacean life including the ability to stun prey (Norris & Mohl, 1981), and the herding of fish (Hult, 1982). Intense echolocation trains termed 'buzzes' have also been described during interspecific encounters between dolphins and sharks (Wood, 1953; Wood *et al.*, 1970). Since Atlantic spotted dolphins used genital buzzes during foreplay, and at a distance, it is possible that this vocalization may have a tactile effect on the recipient, ranging from pain to pleasure, during conspecific interactions as theorized (Johnson & Herzing, 1991; Overstrom, 1983).

Burst-pulsed vocalizations
Many researchers have suggested that pulsed sounds may play a significant role in odontocete communication (Caldwell & Caldwell, 1967; Gish, 1979; Herman & Tavolga, 1980). General correlations between behaviors and burst-pulsed sounds have been reported for bottlenose dolphins including a high intensity, broad-band 'crack' or 'pop' in alarm and fright (Caldwell & Caldwell, 1967), with the herding of females by male coalitions of bottlenose dolphins in Australia (Connor *et al.*, 1992), in head-to-head and agonistic and open-mouth encounters (Caldwell & Caldwell, 1967; Gish, 1979; Herzing, 1988; Overstrom, 1983), in play encounters (Caldwell & Caldwell, 1967), and during disciplinary behavior between mothers and infants (McCowan & Reiss, 1994).

Reports of burst-pulsed vocalizations in other odontocetes include exchanges between Hawaiian spinner dolphins (Norris *et al.*, 1994; Watkins & Schevill, 1974), from pilot whales (*Globicephala malaena*) and harbor porpoise, *Phocoena phocoena* (Busnel & Dziedzic, 1966), during training periods and excited states of Atlantic spotted dolphins (Caldwell & Caldwell, 1971), in narwhals (Ford & Fischer, 1978), and in the use of pulsed codas, thought to carry signature information, in sperm whales, *Physeter macrocephala* (Watkins & Schevill, 1977). These studies suggest that burst-pulsed sounds, like squawks used during intra and interspecific interactions, may be an important, but

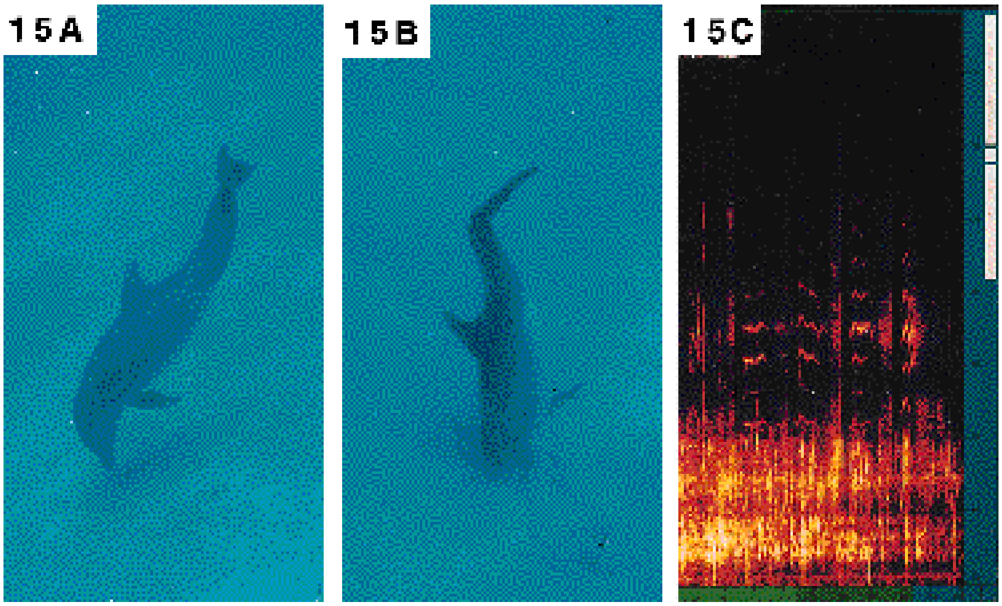


Figure 15. Foraging behavior—bottlenose dolphins. (a and b) Bottlenose dolphin orients and penetrates sand with rostrum; (c) spectrogram of razor buzz during penetration into sand with rostrum. (Clicks appear harmonic in nature due to the high repetition rate of >500 clicks per second [Watkins, 1967].)

often overlooked, part of the vocal repertoire of many odontocetes.

Synchronized squawks/barks
The synchronized squawk, unreported in the literature, was recorded in the Bahamas and was concurrent with synchronized swimming behavior of

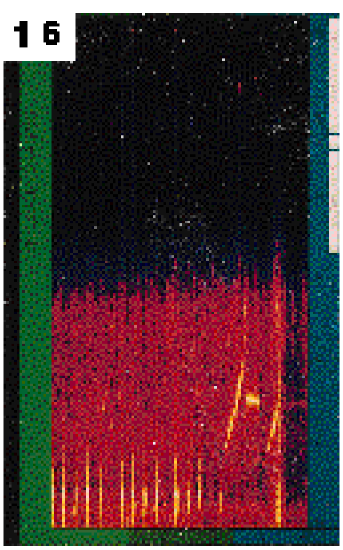


Figure 16. Spectrogram of trills, and upswept whistles during ledge feeding by bottlenose dolphins.

male groups of spotted dolphins during aggressive behavior. The synchronization of behavior and vocalizations has been reported in male bottlenose dolphins during herding behavior of females (Conner *et al*., 1992), episodes of whistling during show behaviors (Firestein *et al*., 1982), and in the coordination of spinner dolphins (Brownlee & Norris, 1994). Synchronization of behavior occurs during strand feeding (Petricig, 1993) and possibly during rhythmic braying (dos Santos *et al*., 1995). Choruses of barks have been reported during interspecific chases in captivity between Atlantic spotted dolphins and bottlenose dolphins and during exposure of dolphins to a tiger shark (Wood, 1953). In some instances, bubble stream emissions were visible for multiple dolphins during this activity. Mammalian patterns of male synchronized behavior during coordinated efforts of activity is also described for various species of primate (Smuts *et al*., 1987) and may warrant more investigation in cetaceans.

Other communicative sounds
Non-vocal impulse sounds have been described spectrally and in behavioral contexts (Marten *et al*., 1988). Tail-slaps and jaw claps have both been described in the context of aggression (Herzing, 1988; Overstrom, 1983) and interspecifically during the intimidation of a subordinate dolphin by dominant conspecifics (Wood, 1953). Bubbles are also considered signals in the repertoire of many species and bubble rings (torus)

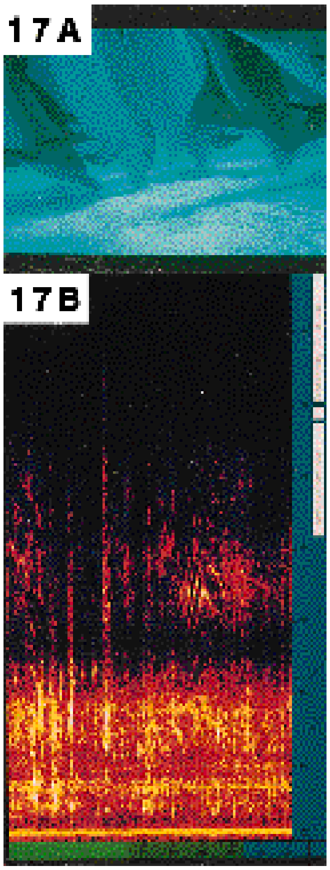


Figure 17. Interspecies foraging behavior. (a) A dense aggregation of spotted and bottlenose dolphins foraging in the bottom; (b) spectrogram of razor buzz with rostra oriented into the sand. (Clicks appear harmonic in nature due to the high repetition rate of 400–500 clicks per second [Watkins, 1967].)

during aggression and other bubble emissions have been described for pantropical spotted dolphins (Pryor & Kang, 1980).

Foraging/feeding vocalizations

Food preferences and hunting strategies have been obtained primarily from sampling stomach content from observations of surface behavior including fish kicking (dos Santos & Lacerda, 1987; Wells *et al.*, 1987) and stranding on mud flats to retrieve fish (Hoese, 1971; Rigley, 1983; Petricig, 1993). In the Bahamas, both bottlenose and spotted dolphins used a specific type of echolocation train, termed the 'razor buzz', during foraging behavior. The use of echolocation signals in the detection and retrieval of prey items is well established and intense sound pressure levels of over 200 dB re1 micro Pa (Au *et al.*, 1978) emitted by bottlenose dolphins may have an effect on prey species (Norris & Mohl, 1981). It should be noted that high-frequency echolocation clicks are very directional (10° from midline) and the maximum frequency recorded during these underwater behaviors may be a limitation of recording equipment and lack of ability to sample in front of the scanning dolphins.

The need for larger frameworks

In addition to the need for more analysis of visual and postural signals in delphinid communication, several larger frameworks in the analysis of general animal communication systems should be considered as originally discussed by Sebeok (1965) and specifically for cetaceans (Tavolga, 1983) including:

(1) Graded signal use: Morton (1977) devised a set of 'structural and motivational' rules, based on the harshness and the frequency of the sound, for the calls of a variety of mammals and birds. This matrix supports the continuous and graded nature of many signals in animal communication.

(2) Prosodic features of sound: Prosodic features of sound, including rhythm, silence, and intensity, may communicate information between conspecifics. Gish (1979) analyzed the temporal relationship of sounds between two bottlenose dolphins and found evidence for a rhythm or cadence where the duration of the last vocalization of one dolphin was highly correlated with the interval before the second dolphin's vocalization period and the duration of the first signal.

(3) Physiological correlates and arousal levels of sound: McConnell (1990) reported, in a study of interspecific acoustic communication, that the most important variations along acoustic continuums were (a) the pulsed vs. continuous nature of sounds, and (b) the slope of frequency modulation within the signal. She further speculated that different acoustic structures have different physiological effects on the internal arousal level of the receiver. This type of response is suggested from evidence from non-human primates (Cleveland & Snowdon, 1982; Struhsaker, 1967), from avian repertoires (Marler, 1982), and bats (Gould, 1983).

(4) Contextual information: The need for more contextual information, including individuals, audience, and relationship, during the use of communicative signals has been emphasized by many researchers (Sebeok, 1965; Smith, 1977; Tavolga, 1983). Learning, memory, development, and the relationship between cognition and communication and its relevance to delphinid communication, has also been thoroughly discussed (Johnson, 1993).

These frameworks suggest that analyzing discrete and graded multi-modal signals, the rhythm and sequence of signals, and social elements that form a 'context' for the animal in an environment, may play a crucial role in the interpretation of communication systems of many animals, including delphinids.

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References

Altmann, J. (1974) Observational study of behavior: sampling methods. *Behavior* **49,** 227–267.

Au, W. W. L., Floyd, R. W. & Haun, J. E. (1978) Propagation of Atlantic bottlenosed dolphin echolocation signals. *J. Acoust. Soc. Am.* **64**(2), 411–412.

Brownlee, S. M. & Norris, K. S. (1994) The acoustic domain. Chapter 8. In *The Hawaiian Spinner Dolphin* (eds K. S. Norris, B. Wursig, R. S. Wells & M. Wursig) pp. 161–185. University of California Press: Berkeley, CA.

Busnel, R. G. & Dziedzic, A. (1966) Acoustic signals of the Pilot whale *Globicephala melaena* and of the porpoises *Delphinus delphis* and *Phocoena phocoena*. In *Whales, Dolphins and Porpoise* (ed. K. S. Norris) pp. 607–648. University of California Press: Berkeley, CA.

Byrnes, P. E., Black, N. A. & Leatherwood, S. (1989) Photo-identification, behavior and distribution of spotted dolphins (*Stenella frontalis*) in the Bahama Banks. *8th Bien. Conf. Biol. Mar. Mam.*, 7 December, 1989, Pacific Grove, CA (Abstract).

Caldwell, D. K. & Caldwell, M. C. (1966) Observations on the distribution, coloration, behavior and audible sound production of the spotted dolphin, *Stenella plagiodon. Contributions in Science* **104,** 1–28.

Caldwell, D. K. & Caldwell, M. C. (1971) Underwater pulsed sounds produced by captive spotted dolphins, *Stenella plagiodon. Cetology* **1,** 1–7.

Caldwell, M. C. & Caldwell, D. K. (1965) Individualized whistle contours in bottlenosed dolphins (*Tursiops truncatus*). *Nature* **207,** 434–435.

Caldwell, M. C. & Caldwell, D. K. (1967) Intraspecific transfer of information via the pulsed sound in captive Odontocete Cetaceans. In *Animal Sonar Systems, Biology & Bionics* (ed. R. G. Busnel) pp. 879–936. Laborative de Physiologie Acoustique: Jouy-en-Josas, France.

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

Caldwell, M. C., Caldwell, D. K. & Miller, J. F. (1973) Statistical evidence for individual signature whistles in the spotted dolphin, *Stenella plagiodon. Cetology* **16,** 1–21.

Caldwell, M. C., Caldwell, D. K. & Tyack, P. L. (1990) Review of the signature-whistle hypothesis for the Atlantic bottlenose dolphin. In *The Bottlenose Dolphin* (eds S. Leatherwood & R. R. Reeves) pp. 199–233. Academic Press: San Diego. 653 pp.

Cleveland, J. & Snowdon, C. T. (1982) Complex vocal repertoire of the adult cotton-top tamarin (*Saguinus oedipus oedipus*). *Z. Tierpsychol.* **58,** 231–268.

Connor, R. C., Smolker, R. A. & Richards, A. F. (1992) Two levels of alliance formation among male bottlenose dolphins (*Tursiops* sp.). *Proc. Natl. Acad. Sci. USA* **89,** 987–990.

de Waal, F. B. M. & Harcourt, A. H. (1992) In *Coalitions and Alliances in Humans and Other Animals* (eds A. H. Harcourt & F. B. M. De Waal) p. 3. Oxford University Press: Oxford.

dos Santos, M. E. & Lacerda, M. (1987) Preliminary observation of the bottlenose dolphin (*Tursiops truncatus*) in the Sado estuary (Portugal). *Aquatic Mammals* **13**(2), 65–80.

dos Santos, M. E., Caporin, G., Moreira, H. O., Ferreira, A. J. & Coelho, J. L. B. (1990) Acoustic behavior in a local population of bottlenose dolphins. In *Sensory Abilities of Cetaceans* (eds J. Thomas & R. Kastelein). Plenum Press: New York.

dos Santos, M. E., Ferreira, A. J. & Harzen, S. (1995) Rhythmic sound sequences emitted by aroused bottlenose dolphins in the Sado estuary, Portugal. In *Sensory Abilities of Cetaceans* (eds J. Thomas, R. Kastelein & P. Nachtigall). De Spil Publisher: Woerden, The Netherlands.

Dreher, J. J. & Evans, W. E. (1964) Cetacean communication. In *Marine Bioacoustics* (ed. W. N. Tavolga) pp. 378–399.

Driscoll, A. D. & Ostman, J. (1991) Categorizing the whistles and choruses of Hawaiian spointter dolphins. *9th Bien. Conf. Biol. Mar. Mam.*, 5–9 December, 1991, Chicago, IL (Abstract).

Dudzinski, K. M., Clark, C. W. & Wursig, B. (1995) Mobile video/acoustic system for simultaneous underwater recording of dolphin interactions. *Aquatic Mammals* **21**(3), 187–193.

Evans, W. E. (1966) Vocalizations among marine mammals. *Marine Bioacoustics* **2,** 159–185.

Firestein, S., Reiss, D., Markowitz, H., Mullen, J. & Silverman, B. (1982) Incidence of spontaneous vocalizations correlated with trained behaviors in captive *Tursiops truncatus. Mar. Mamm. Info*. (ed. B. R. Mate). July 1982.

Ford, J. K. B. & Fisher, H. D. (1978) Underwater acoustic signals of the narwhal (*Monodon monoceros*). *Can. J. Zool.* **56,** 552–560.

Gish, S. L. (1979) Quantitative description of two-way acoustic communication between captive Atlantic bottlenosed dolphins (*Tursiops truncatus montagu*). Doctoral dissertation, University of California, Santa Cruz.

Gould, E. (1983) Mechanisms of mammalian auditory communication. In *Advances in the Study of Mammalian Behavior* (eds J. F. Eisenberg & D. G. Kleiman) pp. 265–342. Spec. Publ. Amer. Soc. Mamm. 7.

Herman, L. M. & Tavolga, W. N. (1980) Communication systems of Cetaceans. *Cetacean Behavior: Mechanisms and Function* (ed. L. M. Herman) pp. 149–197.

Herzing, D. L. (1988) A quantitative description and behavioral associations of a burst-pulsed sound, the squawk, in captive bottlenose dolphins, *Tursiops truncatus*. Masters Thesis, San Francisco State University. 87 pp.

Herzing, D. L. (1989) Social structure and underwater behavioral observations of Atlantic Spotted Dolphins, *Stenella frontalis*, in Bahamian water, 1986–1989. *8th Bien. Conf. Mar. Mam.* 7 December, 1989, Pacific Grove, CA.

Herzing, D. L. (1991) Underwater behavioral observations and sound correlations of free-ranging Atlantic spotted dolphins, *Stenella frontalis*, and bottlenose dolphin, *Tursiops truncatus. 9th Bien. Conf. Biol. Mar. Mam.* 5 December, 1991, Chicago, IL.

Herzing, D. L. (1993) Function of behavior and vocalizations in male coalitions of free-ranging Atlantic spotted dolphins, *Stenella frontalis. 10th Bien. Conf. Biol. Mar. Mam.* 11 November, 1993, Galveston, TX.

Herzing, D. L. (1994) The contextual nature of underwater behavior and vocalizations in Atlantic spotted dolphins *Stenella frontalis. Eur. Res. Cet.* **8,** 156–158.

Herzing, D. L. (1996) The natural history of free-ranging Atlantic spotted dolphins (*Stenella frontalis*): age classes, color phases and female reproduction. *Mar. Mamm. Sci.* In press.

Hoese, H. D. (1971) Dolphin feeding out of water in a salt marsh. *J. Mammal.* **52,** 222–223.

Hult, R. W. (1982) Another function of echolocation for bottlenose dolphins. *Cetology* **47,** 1–7.

Johnson, C. M. (1993) Animal communication by way of coordinated cognitive systems. In *Perspectives in Ethology* (eds P. P. G. Bateson, P. H. Klopfer & N. S. Thompson) pp. 187–205. Plenum Press: New York.

Johnson, C. M. & Herzing, D. L. (1991) Social use of the tactile effects of dolphin vocalizations. *9th Bien. Conf. Biol. Mar. Mam.* 5 December, 1991, Chicago, IL.

Lilly, J. C. & Miller, A. M. (1961) Vocal exchanges between dolphins. *Science* **134,** 1873–1876.

Marler, P. R. (1982) Avian and primate communication: the problem of natural categories. *Neuroscience & Biobehavioral Reviews* **6,** 87–92.

Marten, K. & Norris, K. S. (1988) Loud impulse sounds in odontocete predation and social behavior. In *Animal Sonar* (eds P. Nachtigall & P. Moore) pp. 567–579. Plenum Press: New York.

McBride, A. F. & Hebb, D. O. (1948) Behavior of the captive bottlenose dolphin, *Tursiops truncatus. J. Comp. Physiol. Psychol.* **41,** 111–123.

McConnell, P. B. (1990) Acoustic structure and receiver response in domestic dogs, *Canis familiaris. Anim. Beh.* **39,** 887–904.

McCowan, B. & Reiss, D. (1994) Maternal aggressive contact vocalizations in captive bottlenose dolphins (*Tursiops truncatus*): wide-band, low-frequency signals during mother/aunt–infant interactions. *Zoo Biology* **14,** 293–309.

McCowan, B. & Reiss, D. (1995) Quantitative comparison of whistle repertoires from captive adult bottlenose dolphins (Delphinidae, *Tursiops truncatus*): a re-evaluation of the signature whistle hypothesis. *Ethology* **100,** 194–209.

Morton, E. S. (1977) On the occurrence and significance of motivation structural rules in some bird and mammal sounds. *Amer. Natur.* **111,** 855–869.

Norris, K. S. (1969) Echolocation of marine mammals. In *Biology of Marine Mammals* (ed. H. T. Andersen) pp. 391–423. Academic Press: New York.

Norris, K. S. & Dohl, T. (1980) Structure and function of cetacean schools. In *Cetacean Behavior: Mechanisms and Functions* (ed. L. M. Herman) pp. 230–244. John Wiley & Sons: New York.

Norris, K. S. & Mohl, B. (1981) Can odontocetes stun prey with sound? *Am. Natur.* **122**(1), 85–104.

Norris, K. S., Prescott, J. H., Asa-Dorian, P. V. & Perkins, P. (1961) An experimental demonstration of echolocation behavior in the porpoise, *Tursiops truncatus*, Montagu. *Biol. Bull.* **120,** 163–176.

Norris, K. S., Wursig, B., Wells, R. S. & Wursig, M. (1994) *The Hawaiian Spinner Dolphin* p. 408. University of California Press: Berkeley, CA.

Overstrom, N. A. (1983) Association between burst-pulse sounds and aggressive behavior in captive Atlantic bottlenosed dolphins (*Tursiops truncatus*). *Zoo Biology* **2,** 93–103.

Petricig, R. (1993) Diel patterns of 'strand feeding' behavior by bottlenose dolphins in South Carolina salt marshes. *10th Bien. Conf. Biol. Mar. Mam.* 11 November, 1993, Galveston, TX.

Popper, A. N. (1980) Sound emission and detection by delphinids. In *Cetacean Behavior: Mechanisms and Functions* (ed. L. M. Herman) pp. 1–52. John Wiley & Sons: New York.

Pryor, K. & Kang, I. (1980) Social behavior and school structure in pelagic porpoises (*Stenella attenuata* and *S. longirostris*) during purse seining for tuna. *National Marine Fisheries Service*, SW Fisheries Center, PO Box 271, La Jolla, CA 92038. Adm Report LJ-80-11c. 86 pp.

Pryor, K. & Kang-Shallenberger, I. (1991) Social structure in spotted dolphins (*Stenella attenuata*) in the tuna purse seine fishery in the Eastern Tropical Pacific. In *Dolphin Societies: Discoveries and Puzzles* (eds K. Pryor & K. S. Norris) pp. 161–196. University of California Press: Berkeley, CA.

Puente, A. E. & Dewsbury, D. A. (1976) Courtship and copulatory behavior of bottlenosed dolphins (*Tursiops truncatus*). *Cetology* **21,** 1–9.

Reiss, D. (1988) Observations on the development of echolocation in young bottlenose dolphins. In *Animal Sonar* (eds P. E. Nachtigall & P. W. B. Moore) pp. 121–127. Plenum Publishing Corp.

Rigley, L. (1983) Dolphins feeding in a South Carolina salt marsh. *Whalewatcher* **17**(2), 3–5.

Sayigh, L. S., Tyack, P. L., Wells, R. S. & Scott, M. D. (1990) Signature whistles of free-ranging bottlenose dolphins *Tursiops truncatus*: stability and mother–offspring comparisons. *Behav. Ecol. Sociobio.* **26,** 247–260.

Schultz, K. W., Cato, D. H., Corkeron, P. J. & Bryden, M. M. (1995) Low frequency narrow-band sounds produced by bottlenose dolphins. *Mar. Mamm. Sc.* **11**(4), 503–509.

Sebeok, T. A. (1965) Animal communication. *Science* **147,** 1006–1013.

Simila, T. & Ugarte, F. (1993) Surface and underwater observations of cooperatively feeding killer whales in northern Norway. *Can. J. Zool.* **71**(8), 1494–1499.

Slooten, E. (1994) Behavior of Hector's dolphin: classifying behavior by sequence analysis. *J. Mamm.* **75**(4), 956–964.

Smith, W. J. (1977) *Behavior of Communicating*. Harvard University Press: Cambridge, MA. 545 pp.

Smolker, R. A., Mann, J. & Smuts, B. B. (1993) Use of signature whistles during separations and reunions by wild bottlenose dolphin mothers and infants. *Behav. Ecol. Socio.* **33,** 393–402.

Smuts, B. B., Cheney, D. L., Seyfarth, R. M., Wrangham, R. W. & Struhsaker, T. T. (1987) *Primate Societies*. University of Chicago Press: Chicago, IL.

Struhsaker, T. T. (1967) Auditory communication among vervet monkeys (*Cercopithecus aethiops*). In *Social Communication in Primates* (ed. S. A. Altmann). University of Chicago Press, Chicago, IL.

Tavolga, M. C. & Essapian, F. S. (1957) The behavior of the bottlenose dolphin, *Tursiops truncatus*: mating, pregnancy and parturition, mother–infant behavior. *Zoologica* **42,** 11–31.

Tavolga, W. N. (1983) Theoretical principles for the study of communication in cetaceans. *Mammalia* **47**(1), 3–26.

Watkins, W. A. (1967) The harmonic interval: factor or artifact in spectral analysis of pulse trains. In *Marine Bioacoustics* (ed. W. N. Tavolga) vol. 2, pp. 15–43. Pergamon Press: New York.

Watkins, W. A. & Schevill, W. E. (1974) Listening to Hawaiian spinner porpoise, *Stenella cf. longirostris*, with a three-dimensional hydrophone array. *J. Mammal.* **55,** 319–328.

Watkins, W. A. & Schevill, W. E. (1977) Sperm whale codas. *J. Acous. Soc. Am.* **62**(6), 1485–1490.

Watkins, W. A. & Wartzok, D. (1985) Sensory biophysics of marine mammals. *Mar. Mam. Sci.* **1**(3), 219–260.

Wells, R. S., Scott, M. D. & Irvine, A. B. (1987) The social structure of free-ranging bottlenose dolphins. In *Current Mammalogy* (ed. H. H. Genoways) vol. 1, pp. 247–305.

Wood, F. G. Jr. (1953) Underwater sound production and concurrent behavior of captive porpoise, *Tursiops truncatus* and *Stenella plagiodon. Bull. Mar. Sci. Gulf Carib.* **3,** 120–133.

Wood, F. G., Caldwell, D. K. & Caldwell, M. C. (1970) Behavioral interactions between porpoises and sharks. In *Investigations on Cetacea* (ed. G. Pilleri) vol. II, pp. 264–277.

Wursig, B., Kieckhefer, T. R. & Jefferson, T. A. (1990) Visual displays for communication in cetaceans. In *Sensory Abilities of Cetaceans* (eds J. Thomas & R. Kastelein) pp. 545–559. Plenum Press: New York.