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Acoustics and Social Behavior of Wild Dolphins: Implications for a Sound Society

DENISE L. HERZING

1. Introduction

Understanding and documenting the characteristics and features of the social sounds and associated behavior of free-ranging delphinids has historically been limited by lack of access to animals and poor underwater viewing conditions. Communication studies of delphinids have been undertaken in both captivity (see Herman and Tavolga 1980 for review) and in the wild (Connor et al. 1992; Norris et al. 1994). Even with a wealth of information about dolphin sound production and hearing capabilities from captivity, there are significant gaps in understanding how dolphins detect, decode, and decipher both their environmental and social signals in the wild. Although the abilities of dolphins to actively produce both echolocation signals and social sounds have been documented, little is understood about the sensory exposure and information available to, and utilized by, free-ranging delphinids. One way to address this issue is to review the use of conspecific social signals and behavior. Dolphins, like other animals, have been under evolutionary pressures for increased efficiency in their communication system. By observing critical environmental and social aspects of delphinid society we might gain insight into how these animals learn and selectively filter information in their environment.

This chapter will outline the characteristics of social sounds and associated behavior of delphinids, specifically *Stenella frontalis*, the Atlantic spotted dolphin, and *Tursiops truncatus*, the bottlenose dolphin. These two species have been the focus of a long-term, underwater natural history study in the Bahamas. The major emphasis of this chapter will be on the available information in the dolphin's environment, the contextual use of conspecific vocalizations, developmental behavior, and low-frequency (but sometimes significant event) behavior. Potentially valuable future lines of inquiry into delphinid communication and hearing will be discussed in the last section.

1.1 History of Species Studied in the Wild

It has long been thought that dolphin communication is both complex and contextual (Tavolga 1983; Johnson 1993). 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. This includes the effect of observers or intended recipients of information, the history of the animal, and individual differences (Smith 1977). Because of the highly developed acoustic sense in dolphins, researchers have emphasized the recording and analysis of vocalizations (Evans 1966; Herman and Tavolga 1980). The term "vocalizations," although a misnomer since delphinids do not possess vocal chords, is used in this chapter to describe what should be correctly labeled, the "phonations" of delphinids.

Dolphins communicate using both vocal and nonvocal signals (Würsig et al. 1990). Qualitative descriptions of behavior and associated vocalizations of captive dolphins were reported in early years (Caldwell and Caldwell 1967). Field studies often vary in their access to animals and in the field site conditions, such as the ability to observe from the surface or underwater. Observations of surface behavior of free-ranging dolphins are the most accessible types of observations in the wild, and include general categories of rest, travel, socializing, and feeding (Shane 1990). Basic vocal repertoires have also been accumulated for a variety of species including *T. truncatus* (Caldwell and Caldwell 1967), pilot whales, *Globicephala meleana* (Taruski 1979), Amazon river dolphins, *Inia geoffrensis* (Caldwell et al. 1966), belugas, *Delphinapterus leucas* (Sjare and Smith 1986), spinner dolphins, *Stenella longirostris* (Driscoll 1995), and killer whales, *Orcinus orca* (Ford 1991). Recently, quantitative measures of surface and underwater behavior and vocalizations have been used in studies of free-ranging delphinids (Table 5.1) including *S. longirostris* (Norris et al. 1994; Ostman 1994), pantropical spotted dolphins, *Stenella attenuata* (Pryor and Kang-Shallenberger 1991), *S. frontalis* (Herzing 1996), *O. orca* (Simila and Ugarte 1993; Thomsen 1995), Hector's dolphins, *Cephalorhynchus hectori* (Slooten 1994), and *T. truncatus* (dos Santos et al. 1990; Smolker et al. 1993; Schultz et al. 1995; Connor and Smolker 1996; Oehen 1996). Nevertheless, underwater behavioral observations and associated vocalizations of free-ranging dolphins are difficult. Although early technical arrays (Watkins and Schevill 1974) and later advanced methods (Dudzinski et al. 1995) attempted to localize individual vocalizers, all have had limited success.

Although much progress has been made in understanding the acoustic behavior of many species of dolphins and whales (Tyack and Clark, Chapter 4), associating vocalizations with underwater behavior has proved difficult due to the lack of underwater access to dolphins and their life history, sex, and relationship information. The four species with current underwater and life history observation potential include *S. longirostris*, *S. attenuata*,

TABLE 5.1. Vocalization and behavioral work on free-ranging dolphins

Species	Type of Vocalization	Behavioral Categories	Type of Observation	Location	Reference
<i>Tursiops truncatus</i>	Signature whistle, burst-pulsed	Affiliative Male alliance Consortships Socializing	Underwater and surface	Australia	Connor et al. 1992; Smolker et al. 1993; Connor and Smolker 1996
<i>Tursiops truncatus</i>	Burst-pulsed, low-frequency, narrow-band		Surface	Australia	Schultz et al. 1995
<i>Tursiops truncatus</i>	Whistles, burst-pulsed	Dive, travel, social feed, mill	Surface	Croatia	Oehen 1996
<i>Tursiops truncatus</i>	Burst-pulsed	Arousal Feeding	Surface	Portugal	dos Santos et al. 1990
<i>Stenella attenuata</i>	Whistles, burst-pulsed	Affiliative, Aggressive	Underwater and surface	Eastern Tropical Pacific	Pryor and Kang-Shallenberger 1991
<i>Stenella longirostris</i>	Whistles	Travel, socialize, night, rest, meet, enter, descent, spread	Underwater and surface	Hawaii	Norris et al. 1994; Driscoll 1995
<i>Stenella frontalis</i> / <i>Tursiops truncatus</i>	Whistles, burst-pulsed, echolocation	Affiliative, aggressive, play, courtship, discipline, forage, distress, interspecific	Underwater and surface	Bahamas	Herzing 1996; Rossbach and Herzing 1997
<i>Orcinus orca</i>	Whistles, burst-pulsed	Travel, social, rest, forage, beach rubbing	Surface	British Columbia	Ford 1991; Thomsen 1995
<i>Orcinus orca</i>	Echolocation	Feeding	Underwater and surface	Norway	Simila and Ugarte 1993
<i>Cephalorhynchus hectori</i>	Whistles, burst-pulsed	Sexual, aggressive, play, feeding, aerial	Surface	New Zealand	Slooten 1994

S. frontalis, and *T. truncatus*, and perhaps other tropical and semitropical species yet unexplored.

2. Historical Functional and Structural Classes of Vocal Signals

Delphinid vocalizations have traditionally been divided up into three *structural* types—whistles, burst-pulsed vocalizations, and echolocation clicks—and two *functional* categories—echolocation clicks used for orientation and navigation and burst-pulsed sounds and frequency-modulated whistles used for social signals.

Classification techniques of the vocal repertoire of dolphins have suffered from nomenclature difficulties. Inherent in call classification is the lack of sufficient spectral and structural information to allow comparison or consistency between research. Examples of some common names and spectral features of the acoustic repertoire of selected species are given in Table 5.2. The isolation of individual structural units of sound versus the combined and sequential use between conspecifics also makes understanding the function of vocalizations, and subsequently hearing, difficult. The repertoire of a species is usually viewed as a subset of sounds, with each subset of sound varying over one or more dimensions or parameters such as frequency contour, duration, etc. The lack of data on salient physical and structural features of vocalizations, and contextual differences, makes understanding the function of such communication signals challenging. The relationship between basic behavioral categories and acoustic characteristics of social sounds can be seen in Fig. 5.1.

Frequency-modulated whistles have been extensively analyzed due to the relative ease of analysis of their discrete features such as contour, frequency modulation over time, duration, and peak frequency (see Caldwell et al. 1990). Whistles tend to be continuous, narrow-band signals with harmonic features. Many whistles in the literature are described as being below the 20kHz level but this may be a function of limited bandwidth recording equipment. Although echolocation click studies have utilized instrumentation recorders to capture ultrasonic information, recent broadband recording of the social sounds of *S. longirostris* have shown the existence of information above 20kHz in both whistles and other social sounds (Lammers and Au 1997).

Burst-pulsed sounds have been much neglected in the literature, although they comprise the majority of conspecific vocalizations. Burst-pulsed sounds are broadband, discrete aural packets of clicks and have acquired descriptive names such as squawks, bleats, barks, etc. Spectral features of burst-pulsed sounds have been analyzed for a few species (Overstrom 1983; Sjare and Smith 1986; Herzing 1988, 1996) but the nature of their informational content is largely unknown. Analyses have been particularly plagued

TABLE 5.2. Representative overview of vocal and nonvocal acoustic signal repertoires of selected species

Type of Signal and Characteristics	Species	Captive or Wild	Behavioral Context	Reference
Vocal				
<i>Whistles (duration > 1 s, frequency ranges 2-18 kHz+, and may be modulated)</i>				
Frequency-modulated whistles/loops (single or multiple loops usually >2 kHz, <18 kHz)	<i>G. melana</i>	Wild	Various	Taruski 1979
	<i>T. truncatus</i>	Wild	Various	Smolker et al. 1993
	"	"	Various	Schultz and Corkeron 1994
	"	"	Reunions	Wang et al. 1995
	<i>S. longirostris</i>	Wild	Night, spread travel	Norris et al. 1994
	<i>S. frontalis</i>	Wild	Reunions, alloparental, courtship	Herzing 1996
	<i>S. frontalis/T. truncatus</i>	Captive	Fear, separation	Wood 1953
	<i>O. orca</i>	Wild	Socialize	Ford and Fisher 1983
	<i>D. leucas</i>	Wild	Contact, coordination	Sjare and Smith 1986
	<i>M. monoceros</i>	Wild	Socialize	Ford and Fisher 1978
Chirps/squeaks (4-8 kHz, .05-1 s, ascending/descending)	<i>T. truncatus</i>	Wild	Foraging	Herzing 1996
Screams (5.8-9.4 kHz, 2.5-4 s) overlapping FM whistles	<i>T. truncatus</i>	Wild	Arousal	dos Santos et al. 1995
	<i>S. frontalis</i>	Wild	Intra- and interspecies aggression	Herzing 1996
	<i>S. longirostris</i>	Wild	Intra- and interspecies aggression	Norris et al. 1994
			Nighttime	
<i>Burst-pulsed (Rapid onset/offset, discrete in time with tonal quality due to higher repetition rates than individual clicks. Broadband in frequency with some emphasis on the lower frequencies)</i>				
Sounds less than 1 s and most energy below 2 kHz, with varying repetition rates				
Cracks (broadband, <1 s)	<i>T. truncatus</i>	Captive	Fear	Caldwell and Caldwell 1967
	<i>I. geoffrensis</i>	Captive	Alarm	Caldwell, Caldwell, and Evans 1966
	<i>T. truncatus</i>	Captive	Fear	Caldwell and Caldwell 1967
	<i>T. truncatus</i>	Wild	Consortship	Connor and Smolker 1996

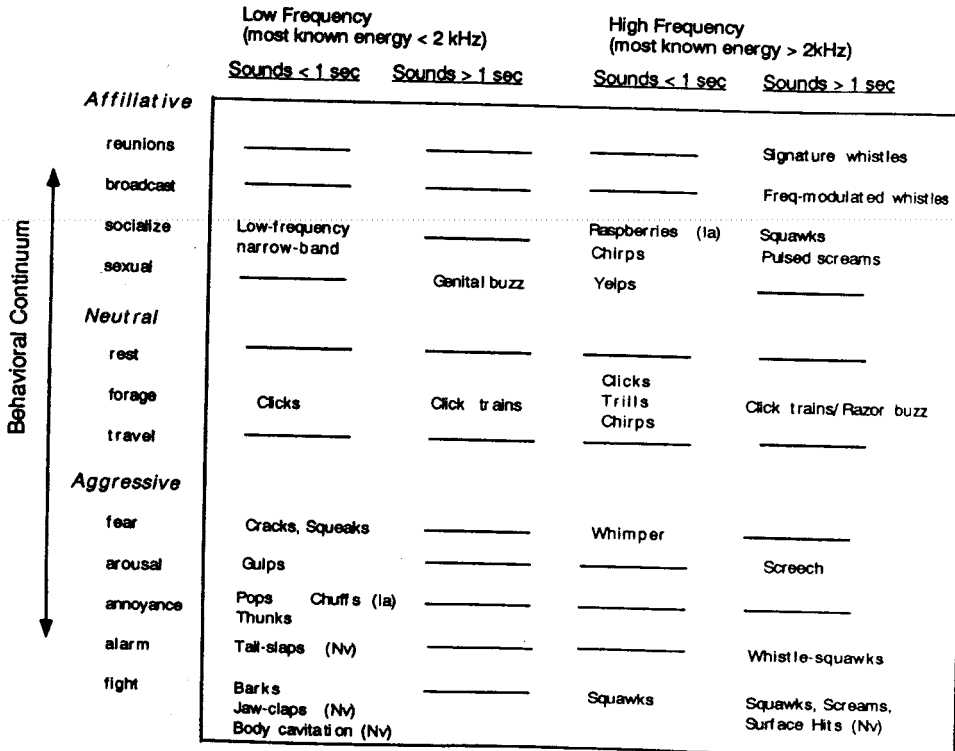
TABLE 5.2. Continued

Type of Signal and Characteristics	Species	Captive or Wild	Behavioral Context	Reference
Barks (<1 s, energy below 2 kHz with frequency drop at end of signal)	<i>S. frontalis</i>	Wild	Aggression	Herzing 1996
Squeaks (<2 kHz, <.1 s)	<i>I. geoffrensis</i>	Captive	NIA	Caldwell, Caldwell, and Evans 1966
Thunks (<2 kHz, <.5 s)	<i>S. plagiodon/T. truncatus</i>	Captive	Aggression	Wood 1953
Gulps (<300 Hz, <.2 s)	<i>T. truncatus</i>	Captive	Alarm	Caldwell and Caldwell 1967
Low-frequency narrow-band (<2 kHz, <.5 sec)	<i>T. truncatus</i>	Wild	Chase	McCowan and Reiss 1994
Trills (2-8 kHz, .03-.5 s)	<i>T. truncatus</i>	Wild	Arousal	dos Santos et al. 1995
Sounds >.1 s with most energy above 2 kHz, with varying repetition rates	<i>T. truncatus</i>	Wild	Socialize	Schultz et al. 1995
Pulsed screams (to 25 kHz, .5-10 s)			Foraging	Herzing 1996
Squawks (.2-12 kHz, .2-1 s) (<6 kHz, .5-1.4 s)	<i>O. orca</i>	Wild	Socialize	Ford and Fisher 1983
Whimper (freq. descending, .3-1 s)	<i>S. frontalis</i>	Wild	Aggression/sexual play	Herzing 1996
Whistle-squawks (4-18 kHz, >.1 s)	<i>T. truncatus</i>	Captive	Fights/play	Caldwell and Caldwell 1967
	<i>I. geoffrensis</i>	Captive	Fear	Caldwell and Caldwell 1967
	<i>T. truncatus</i>	Captive	NIA	Caldwell, Caldwell, and Evans 1966
	<i>T. truncatus</i>	Captive	Distress	Caldwell and Caldwell 1967
	<i>S. frontalis</i>	Captive	Contact	Reiss 1988
	<i>T. truncatus</i>	Wild	Excitement	Herzing 1996
Yelps (up to 6 kHz, .2-1 s)	<i>T. truncatus</i>	Captive	Courtship	Wood 1953
Rasps/mewing (NIA)	<i>T. truncatus</i>	Captive	Sexual play	Caldwell and Caldwell 1967
Screech (up to 6 kHz, .1-2 s)	<i>S. frontalis/T. truncatus</i>	Captive	Feeding	Wood 1953
	<i>T. truncatus</i>	Wild	Arousal	dos Santos et al. 1995
	<i>I. geoffrensis</i>	Captive	NIA	Caldwell, Caldwell, and Evans, 1966
Clicks (Broadband, short in duration, usually long sequences. Varying repetition rates, some individually distinct, others with higher repetition rates have an aural quality)				
Grate/Rusty Hinges (Broadband, <30 clicks/s)	<i>I. geoffrensis</i>	Captive	NIA	Caldwell, Caldwell, and Evans 1966
	<i>S. frontalis/T. truncatus</i>	Captive	Explorations	Wood 1953

Clicks/click trains (20–380 clicks/s)	<i>T. truncatus</i>	Wild	Scanning	dos Santos et al. 1990
Creaks (<280–380 clicks/s, often <2.5 kHz)	<i>I. Geoffrensis</i>	Captive	NIA	Caldwell, Caldwell, and Evans 1966
	<i>T. truncatus</i>	Wild	Various	dos Santos et al. 1990
Moans (>380 clicks/s)	<i>T. truncatus</i>	Wild	Arousal	dos Santos et al. 1990
Genital buzz (8–2,000 clicks/s, <2.5 kHz)	<i>S. frontalis</i>	Wild	Courtship, discipline, chase	Herzing 1996
	<i>T. truncatus</i>	Wild	Foraging	Herzing 1996
Nonvocal				
<i>(Generally noise or cracks of sound not modulated by vocal mechanisms. Loud, longer than individual clicks, and emphasis on low-frequency components.)</i>				
Tail slaps/cracks (<2 kHz main energy, <.5 s)	<i>T. truncatus</i>	Captive	Alarm	Caldwell et al. 1962
	<i>S. frontalis</i>	Wild	Fight	Marten et al. 1988
Body cavitation (<1.4 kHz, <.2 s)	<i>O. orca</i>	Captive	Movement	Marten et al. 1988
	<i>O. orca</i>	Captive	Movement	Marten et al. 1988
Surface hits/aerial jumps (<1 kHz, <.1 s)	<i>S. frontalis</i>	Wild	Aggression	Marten et al. 1988
	<i>S. frontalis</i>	Wild	Annoyance	Herzing 1996
Bubbles (NIA)	<i>S. attenuata</i>	Wild	Frustration	Pryor and Kang-Shallenberger 1991
	<i>S. frontalis/T. truncatus</i>	Captive	Dominance	Wood 1953, Overstrom 1983
Jaw claps (Broadband, most energy <2 kHz, <.5 s)	<i>S. frontalis/T. truncatus</i>	Wild	Aggression, foraging	Herzing 1996
	<i>I. Geoffrensis</i>	Captive	Feeding	Caldwell, Caldwell, and Evans 1966

*NIA = no information available.

Note: limited bandwidth recording equipment may have restricted frequency ranges of many vocalizations.



* Ia = In-air vocalizations, Nv = non-vocal sounds

FIGURE 5.1. The relationship of acoustic features, including frequency and duration, to a changing behavioral continuum, shows a pattern of low-frequency, short-duration vocalizations with escalating aggression and high-frequency, long vocalizations with increasing affiliative behavior. Such patterns have also been observed in other species of mammals and birds (Morton 1977).

by difficulties with categorization artifacts of both human hearing and analysis equipment (Watkins 1967). For example, orca screams, which appear structurally like whistle contours, are actually burst-pulsed streams at very high repetition rates (Ford 1991).

Clicks, click trains, and burst-pulsed sounds lie on a continuum relative to their repetition rates and spatial separation. It is unclear at what rate dolphins perceive individual clicks, and if clicks are functionally different from burst-pulsed packets of clicks in the auditory system of the dolphin. The same spatio-temporal information available about a prey item may also be available to a conspecific and give the receiver valuable social and emotive information, available for social negotiation or decision-making processes. The relative loudness, duration, and number of vocalizations over time may

all be critical information for a receiver. Some species of Cetacea use click trains for both navigation and social purposes (Dawson 1991; Richardson et al. 1995). Many dolphins species emit high-frequency click trains during echolocation and orientation tasks, but the existence and use of these components in social contexts are unexplored.

2.1 *Categorical Issues of Perception*

Basic psychoacoustics (Nachtigall et al., Chapter 8), physiology (Ridgway, Chapter 6), and electrophysiological aspects of auditory processing (Dolphin, Chapter 7) are described. There has been little experimental work on categorical perception by dolphins to conspecific sounds or to the critical features and parameters of artificially created sounds. Recent anatomical (Cranford et al. 1996, and Chapter 3; Ketten, Chapter 2), structural (McGowan and Reiss 1995; Murray 1997), and behavioral (Norris et al. 1994; Herzing 1996) evidence suggests that both our analysis techniques and previous human categorical tendencies may not best describe delphinid vocalizations.

The lack of consistent and perceptually accurate categories of delphinid vocalizations may represent methodological difficulties inherent both in the human ear and analysis equipment (Watkins 1967). Our ability to discriminate individual clicks and high-repetition-rate pulsed sounds is limited, and burst-pulsed sounds have, in the past, been given a variety of names based on aural characteristics. Recent techniques in analyzing graded signals (Murray 1997) may indicate more quantitative and comparable methods.

In addition to analyzing the psychoacoustics of dolphins, we need to explore their "social acoustics," or use of conspecific vocalizations and sounds. A bias toward the analysis of low-frequency, frequency-modulated whistles has limited our understanding of the full repertoire and complexity of delphinid signal repertoires. Looking at the functional use of communication signals in the wild may be productive in assessing potential categories used and heard by delphinids. How do dolphins perceive the social vocalizations of their conspecifics? It has been demonstrated that dolphins discriminate pitch, duration, frequency, frequency modulation, amplitude modulation, contour, intersound interval, sequencing patterns, and octave adjustments (Ralston and Herman 1989). However, the decoding of these potentially salient features within delphinid social vocalizations is unexplored.

Natural categories of vocalizations in behavioral contexts yield potential information about boundaries for dolphin conspecific sound use. Preferred range of frequency, duration, intensity, signals relations, and intersignal space should be analyzed while including the behavioral context and age classes of individuals utilizing such signals. Developmental aspects of signal use (i.e., generalized versus refined acoustic features) are apparent in vervet

monkey society (Seyfarth and Cheney 1980) and warrants caution in dolphin research. Factors beyond the structure of the call itself include gender, age class, social context, developmental status, and, possibly, reproductive status. Difficulties in documenting contextual information, combined with the lack of ultrasonic recordings of conspecific social vocalizations (as a potential location for supplemental or modulated information), may be responsible, methodologically, for our lack of information on the details of the hearing of conspecific vocalizations.

3. Atlantic Spotted Dolphin Vocal and Nonvocal Repertoire

The basic life history, age class categories, and behavioral habits for *S. frontalis* have recently been described (Herzing 1996, 1997). A sympatric species, *T. truncatus*, also shares the same habitat (Herzing and Johnson 1997; Rossbach and Herzing 1997). Previous studies on the behavior and vocalizations of *S. frontalis* in captivity also exist (Wood 1953; Caldwell and Caldwell 1966, 1971; Caldwell et al. 1973). Due to the lack of observations of most delphinid species under natural social conditions, there remains a significant gap of understanding in the most basic functional and developmental aspects of the hearing and use of conspecific vocalizations.

Following is a detailed account of vocalizations and associated underwater behavior of *S. frontalis* in various age classes, relationships, and during interspecific interactions with bottlenose dolphins. Like many social species, *S. frontalis* employ vocalizations and postural behavior in a wide range of behavior contexts. Although many vocalizations under analysis are within human audible range, there has been little work done on the presence of ultrasonic information during the use of social sounds. Most data are taken from Herzing (1996), and a summary of these vocalizations and contextual information can be found in Table 5.3. Analysis of the full repertoire and contextual use of vocalizations of this species should eventually yield a functional description of these communication signals and how they relate to the hearing abilities of delphinids in the wild.

3.1 Vocalizations Associated with Contact, Reunions, and Broadcasting

Frequency-modulated whistles are the predominant vocalizations heard during behavioral contexts including (1) mother/calf reunions—mothers produce their own signature whistle after calves depart and until they rejoin her; (2) alloparental care—older conspecifics, including male and female dolphins, produce their own signature whistles prior to the retrieval of younger dolphins; (3) courtship behavior—females and males repetitively

TABLE 5.3. *Stenella frontalis* and *Tursiops truncatus* vocalizations and behavior

Type	Common Name	Spectral	Behavioral Context	Species/Age/Sex
Frequency modulated whistles	Signature whistle	4-18kHz .5-8s	Mother/calf reunions, courtship, alloparental	Sf, all ages, M/F
	Screams	5.8-9.4kHz 2.5-4.0s	Agonistic/aggressive	Sf, Tt, juvs, adults, M
Burst-pulsed	Chirps	4-8kHz, .05-1s	Mother/calf, affiliative	Sf
	Excitement vocalization	4-18kHz 2-30s	Distress/excitement	Sf, all ages, M/F
	Squawk	2-12kHz 2-1.0s	Agonistic/aggressive	Sf, Tt, all ages, M/F
Click trains	Bark	2-2.0kHz 5-1.0s	Agonistic/aggressive	Sf, Tt, juvs and adults, M
	Synchronized squawk	.1-15kHz .9-1.0s	Agonistic/aggressive	Sf, Tt, juvs and adults, M
	Genital buzz	1.2-2.5kHz 6-20s	Courtship, discipline, chase	Sf, Tt, juvs and adults, M/F
	Razor buzz	8-2,000 clicks/s 2.0-6.0kHz Sustained 200 clicks/second	Foraging, feeding	Tt
In-air vocalizations	General trains	2.0-6.0kHz 8-100 clicks/s	Foraging, play	Sf, all ages, M/F
	Chuffs	NIA	Annoyance	Sf, Tt, adults
Nonvocal acoustic signals	Raspberries	NIA	Interspecific interaction	Sf, all ages, M/F
	Tail slap	Broadband, most energy <2kHz, <.5s	Discipline, annoyance, Attention	Sf, Tt, all ages, M/F
	Jaw clap	Broadband, most energy <2kHz, <.3s	Aggression Foraging	Sf, Tt, adults, M
	Bubbles	NIA	Courtship, aggression, vocalizing	Sf, all ages, M/F

(Sf = *Stenella frontalis*; Tt = *Tursiops truncatus*; M = Male; F = Female; NIA = no information available.)

broadcast their signature whistles during attempted courtship and mating activity; and (4) individual separation from the group—solitary dolphins, apparently separated from the group, take a position on or near the bottom and emit their signature whistle for minutes while rotating their head. It is unclear whether the dolphins are waiting for a response from a conspecific or broadcasting to members of their group. Recent speculations (Payne and Webb 1971) on the function of long-distance, low-frequency-modulated signals from large balenopterid whales for an “echo-ranging” function (by hitting long-distance targets such as underwater seamounts) challenges our traditional thoughts about the possible uses of frequency-modulated vocalizations.

Whistles are thought to display relatively low directionality as long-distance social communicative signals due to their highly modulated frequency characteristics (Norris and Dohl 1980) and may broadcast individual identity and help maintain or initiate contact between individuals (Smolker et al. 1993; Tyack 1993; Herzing 1996). This is supported by both the stability of whistle contours over the years and kin-related identifiers in whistles (Sayligh et al. 1990). Emotive information possibly contained in such whistles has also been explored (Caldwell and Caldwell 1967; Reiss 1988; Herzing 1996). The use of bubble streams as identifiers of both the individual vocalizing and as representative of the full repertoire of whistles has been verified (McCowan and Reiss 1995). However, recent theories on the possible continuum of clicks and whistles, and the inherent directionality of the sound production mechanism of clicks, challenges the idea that whistles are always, if at all, omnidirectional (Murray 1997).

Other general associations between whistles and behavior include increased whistling rate during excitement and stress in *S. longirostris* (Norris et al. 1994), during bow riding and feeding in the common dolphin, *Delphinus delphis* (Busnel and Dziedzic 1966), during feeding in *Globicephala* sp. (Dreher and Evans 1964), during fleeing and cooperative behavior (Evans 1966), and during mother/infant reunions in *T. truncatus* (Smolker et al. 1993).

Caldwell and Caldwell (1965) first suggested, and later revised (Caldwell et al. 1990), that repetitive whistles, termed “signature” whistles, may be individually specific and may function as identifiers of individual dolphins. Signature whistles have already been described for captive *S. frontalis* (Caldwell et al. 1973). Recently, an expansion/replacement theory termed “whistle repertoire” theory, which normalizes all whistles to their common features and acknowledges the contextually appropriate social situations for whistle use, has recently been proposed (McCowan and Reiss 1995). Although some individual *S. frontalis* have a unique and predominate distinctive whistle, new quantification and normalization techniques described above have not yet been applied to these data. But the existence and stability of “signature” whistles, as described by Sayligh et al. (1990),

should not discount the possibility that there are other social uses of frequency-modulated whistles.

3.2 Vocalizations Associated with Excitement, Distress, and Alarm

The "whistle-squawk" and sharp clicks are the predominate vocalizations produced during behavioral contexts of alarm and distress. *S. frontalis* produce an "excitement vocalization," a combination burst-pulsed sound (in the lower 4 to 8kHz range) and signature whistle of the vocalizer (8 to 18kHz). The duration of this vocalization ranges from 2 to 30s. During the production of this vocalization, dolphins are highly erratic in their swimming behavior and emit a stream of bubbles. The trigger for distress behavior varies from intraspecific social behavior to the presence of human observers in the water. After the production of the vocalization begins, a conspecific makes tactile contact, after which the excitement vocalization ceases. Although counterintuitive, this vocalization has not been observed in the presence of a predator such as a shark. Instead, there is some degree of urgency when conspecifics calm down an excited cohort, indicating the need to avoid broadcasting.

The excitement vocalization is similar in structure to the whistle-squawk described by Caldwell and Caldwell (1967) who reported that *T. truncatus*, when removed from the water, emitted this vocalization. They suggested that this type of sound is emitted when the dolphin is "protesting." 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 *T. truncatus*, and suggested that these sounds are produced during emotional behavior.

Sharp clicks with rapid onset times, including nonvocal sounds such as tail-slaps and even camera clicks from researchers, elicit startle responses in *S. frontalis*. Dolphins are known to have an enhanced sensitivity to short duration, rapid rise-time stimuli (Bullock et al. 1968; Bullock and Ridgway 1972). Dolphins are good at temporal and spatial resolution and are sensitive to small changes in intensity (Ralston and Herman 1989) indicating that they may be very adept at deciphering incremental changes in both time and intensity or amplitude of a signal. It is likely these skills are utilized in ambient noise and environmental assessment, but may also play a role in deciphering social sounds of conspecifics.

The behavior of *S. frontalis* in the presence of sharks, a potentially alarming context, has rarely been observed. In the Bahamas, *S. frontalis* share habitat with at least four major predatory sharks, and limited observations over 12 years indicate that dolphins take different strategies according

to the species and, perhaps, the behavior of the predator. In most cases, dolphins are silent in the presence of sharks, at least within the human audible range. With large groups of mixed-age classes, dolphins sink to the bottom, closely gather, and swim in the opposite direction. With dyads or small subgroups of dolphins, they may lay motionless on the bottom as the shark passes by. In one instance, a mother who had recently been wounded by a shark and apparently was in a state of hypervigilance with her calf, began using an excitement vocalization in murky water when a nurse shark (*Ginglymostoma cirratum*), a harmless species, came into view. In other instances, *S. frontalis* have been observed swimming in the company of large tiger sharks. During these times the dolphins may be discriminating between hunting and nonhunting predators by monitoring the predator in their presence rather than fleeing, indicating that subtle cues may be perceived about the intention of the predator.

3.3 Vocalizations Associated with Pursuit, Herding, and Discipline

During the pursuit and herding of conspecifics the predominant vocalization produced is the "buzz" or "genital buzz." This vocalization is a low-frequency, high-repetition-rate echolocation train that is directed toward the genital or midsection of a conspecific, often by a male to a receptive female during courtship behavior. This vocalization ranges from 1.2 to 2.5 kHz, with durations up to 20s and repetition rates of eight clicks per second up to 2,000 clicks per second.

A similar type of buzz is used when individuals are disciplining others. When mothers are unsuccessful in retrieving their calves, they swim inverted and buzz the genital/peduncle area of their offspring, eventually making physical contact with their rostra. Larger groups of dolphins are observed in tight physical contact, with their rostra pointed toward, but not touching, another dolphin, while they buzz the genital/peduncle area of the individual, who initially tries to swim away from the group. When physical contact of their rostra to the individual's body is finally made, the single dolphin becomes passive and allows itself to be pushed around by the group. In some instances, the single dolphin is held down to the bottom, similar to disciplinary actions between a mother and calf. This behavioral sequence is observed both intraspecifically within and between all age classes of *S. frontalis*, and interspecifically between juvenile and young adult spotted dolphins and *T. truncatus*. The buzz is also used by the dolphins when chasing sharks.

Although this genital buzz described for *S. frontalis* is not found in the literature, echolocation trains termed a "buzz" have been reported in threat situations (Lilly and 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, Floyd and Haun 1978; Norris et al. 1961). Although echolocation and click trains have 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 and Møhl 1981), the herding of fish (Hult 1982), and in tactile stimulation (Johnson and Herzing 1991). Intense echolocation trains, termed "buzzes," have also been described during interspecific encounters between dolphins and sharks (Wood 1953; Wood et al. 1970). Since *S. frontalis* use 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.

3.4 Vocalizations Associated with Agonistic and Aggressive Behavior

The predominant vocalizations produced during agonistic or aggressive behavior are burst-pulsed sounds. Squawks are by far the dominant vocalization during head-to-head confrontations, body charges, and open-mouth posturing. Torus bubbles displays (bubble rings) are also observed. Squawks are broadband, burst-pulsed sounds, and range in frequency from 0.2 to 12 kHz, although the main energy is found in the lower frequencies of 1.1 to 2.4 kHz. Duration ranges from 0.2 to 1.0s with repetition rates from 200 to 1,200 clicks per second. No consistent classification scheme exists for burst-pulsed sounds, and the literature is replete with common names as seen in Table 5.2.

Barks, a low-frequency, burst-pulsed vocalization that ranges from 0.2 to 2.0 kHz and from 0.5 to 1.0s in duration, and screams, overlapping frequency-modulated whistles that range from 5.8 to 9.4 kHz and 2.5 to 4.0s in duration, are also produced during highly escalated agonistic or aggressive behavioral sequences described above.

Many researchers have suggested that pulsed sounds may play a significant role in odontocete communication (Caldwell and Caldwell 1967; Gish 1979; Herman and Tavolga 1980). General associations between behaviors and burst-pulsed sounds have been reported for *T. truncatus*, including a high-intensity, broadband "crack" or "pop" in alarm and fright (Caldwell and Caldwell 1967) and during the herding of females by male coalitions (Connor and Smolker 1996); squawks in head-to-head and agonistic and open-mouth encounters (Caldwell and Caldwell 1967; Gish 1979; Overstrom 1983; Herzing 1988, 1996) and in play encounters (Caldwell and Caldwell 1967); and "thunks" during disciplinary behavior between mothers and infants (McCowan and Reiss 1994).

Reports of burst-pulsed vocalizations in other odontocetes include exchanges between *S. longirostris* (Watkins and Schevill 1974; Norris et al.

1994), *G. malaena* and harbor porpoise, *Phocoena phocoena* (Busnel and Dziedzic 1966), during excited states of *S. frontalis* (Caldwell and Caldwell 1971), in narwhals, *Monodon monoceros* (Ford and Fisher 1978), and in the use of pulsed codas, thought to carry signature information, in sperm whales, *Physeter macrocephala* (Watkins and Schevill 1977). These studies suggest that burst-pulsed sounds are an important, but often overlooked, part of the vocal repertoire of many odontocetes.

3.5 Vocalizations Associated with Group Synchrony and Cohesion

Predominant vocalizations produced during synchronized activity or group mediation include the coordinated production of squawks. In highly escalated aggressive activity, male *S. frontalis* coordinate their swimming behavior, postures, and squawks. Synchronized squawks are a highly coordinated burst-pulsed vocalization that ranges in frequency from 0.1 to 15 kHz, with main energy from 0.1 to 2.2 kHz, and durations from 0.9 to 1.0 s. Young males show partial synchronization of swimming behavior and squawks but are not fully coordinated in their efforts.

The synchronized squawk, unreported in the literature, is associated with close-proximity synchronized swimming behavior of male groups of *S. frontalis* during aggressive behavior. The synchronization of behavior and vocalizations has been reported in male *T. truncatus* during herding behavior of females (Connor et al. 1992), episodes of whistling during show behaviors (Firestein et al. 1982), in the coordination of *S. longirostris* (Brownlee and Norris 1994), and in the rhythmic braying of *T. truncatus* (dos Santos et al. 1995). Choruses of barks have been reported during interspecific chases in captivity between *S. frontalis* and *T. truncatus* and during exposure of dolphins to a tiger shark (Wood 1953). Strong patterns of synchrony in male *S. attenuata* in tuna nets have also been reported (Pryor and Kang-Shallenberger 1991). Mammalian patterns of male synchronized behavior during coordinated efforts of activity are described for various species of primate (Smuts et al. 1987) and in the escalating pep rallies of wild dogs as signals of readiness to fight (Estes and Goddard 1967) and therefore may warrant more investigation in Cetacea.

3.6 Vocalizations Associated with Interspecific Interactions

During sexual play or agonistic or aggressive interactions, squawks and synchronized squawks (when groups of male *S. frontalis* face off with solitary or small groups of *T. truncatus* and chase them as a solidified group) are the predominant vocalization. The scream and bark are also produced during highly escalated agonistic or aggressive behavior between male dolphins

of both species during interspecific conflict (Herzing 1996; Herzing and Johnson 1997).

Many species utilize acoustic information from neighboring species (Fagan 1981). Studies on the perception of the human voice by nonhuman animals (as reviewed in Ralston and Herman 1989) indicate that species-specific processes are not necessary for the recognition of acoustic phonetic segments. Two sympatric species as closely related as *S. frontalis* and *T. truncatus* may be able to decipher species-specific signaling and perhaps use it functionally during mixed-species aggregations. Cross-species signal content may be read across species boundaries utilizing specific sound parameters (Morton 1977). Cross-species overlap may allow messages and their modulated information, to be decoded between species and might provide a research window for decoding information available to both species.

3.7 Nonvocal Acoustics Associated with Behavioral Activity

S. frontalis use (1) tail-slaps as attention-getting mechanisms or in annoyance, (2) jaw claps in escalated aggression, (3) aerial displays during play behavior and also during intra- and interspecific aggressive chases, (4) bubble displays in the production of whistles (bubble trails) and in annoyance (full and half bubbles) and bubble rings (torus) during annoyance or aggressive contexts, and (5) in-air vocalizations, including the chuff (an explosive exhalation) during annoyance and raspberry (a constricted exhalation) in interspecies affiliative contexts. Although nonvocal by traditional definition, these sounds provide acoustic signals and their prosodic features, including rate, spacing, and frequency, may be conserved and available for analysis.

Jaw claps have been noted in aggressive contexts for *T. truncatus* (Overstrom 1983; Herzing 1988) and interspecifically during the intimidation of subordinate dolphins by dominant conspecifics (Wood 1953). Sharp puffs of air have been noted during signs of agitation by *S. attenuata* (Pryor and Kang-Shallenberger 1991). Bubbles and bubble rings (torus) are produced during aggressive interactions of *S. attenuata* (Pryor and Kang 1980) and during play activity of *T. truncatus* (Marten et al. 1996).

Nonvocal impulse sounds, including sounds produced by slamming of body parts, cavitation movements, percussive thrashing during attempted hits, closure of the jaw, and various aerial behaviors, have been described spectrally and in behavioral contexts for multiple species (Marten et al. 1988) and during behavioral contexts including agitation and stress (Caldwell et al. 1962; Norris and Dohl 1980; Pryor and Kang-Shallenberger 1991). Such signals are typically of a short time duration and may function as supplemental or exclamatory signals during activity, either from a distance or in close proximity. Wild dolphins may be able to convey, as

well as extract, important information through the use of aerial behaviors, percussive sounds associated with body and tail movements underwater, and species- and movement-specific information from prey, conspecifics, or allospecifics as documented in bats (Kober 1988; von der Emde 1988).

3.8 Vocalizations Associated with Foraging and Feeding

Predominant vocalizations produced during hunting and foraging behavior are echolocation clicks. *S. frontalis* and *T. truncatus* echolocate while scanning and digging for buried prey in sandy bottoms, increasing the repetition rate of clicks (from 200 to 500 clicks per second) as they direct their sound into the sand. Bottom fish appear to be disoriented or stunned as they emerged from the sand and become easy prey for the dolphins. *T. truncatus* use an echolocation train termed the "razor buzz" (aurally distinguishable from other echolocation click trains by the intensity and "tinny" quality), ranging from 2.0 to 6.0 kHz with repetition rates up to 200 clicks per second (Herzing 1996). *T. truncatus* also use the razor buzz in conjunction with trills (repetitive series of discrete beeps below 5.0 kHz) and upswept whistles (ranged from 4.8 to 16.0 kHz) during "ledge" feeding, although these may serve another functions such as conspecific or coordination vocalizations. In addition, dolphins use jaw claps and open-mouth scanning during hunting and foraging behavior.

Food preferences and hunting strategies have been obtained primarily from sampling stomach content and from observations of surface behavior including fish kicking (dos Santos and Lacerda 1987; Wells et al. 1987) and stranding on mud flats to retrieve fish (Hoese 1971; Rigley 1983). The use of echolocation signals in the detection and retrieval of prey is well established, and intense sound pressure levels of over 220 dB re 1 μ Pa (Au et al. 1978, Au 1993) emitted by *T. truncatus* may have an effect on prey species (Norris and Møhl 1981), although it has not been experimentally demonstrated. It should be noted that high-frequency echolocation clicks are very directional (10° from mid-line) and the maximum frequency recorded during these underwater behaviors may be a limitation of recording equipment and the lack of ability to sample in front of the scanning dolphins. Preliminary evidence that *S. frontalis* use clicks up to 140 kHz and 210 dB re 1 μ Pa has also been documented (Au et al. 1998).

3.9 Acoustic Characteristics of Social Sounds Relative to Hearing

A summary of both Table 5.2 and Figure 5.1 indicate that dolphin social signals share some structural traits that may both relate to their function and show conservation during the evolution of communication signals across species. Sounds with sharp onset and energy emphasis in the lower

frequencies are found in fear, arousal, and alerting contexts. Sounds with discrete time features, stretching broadband frequency widths, are found in a variety of contexts including excitement, feeding, and aggressive displays. Finally, longer vocalizations, modulated by frequency, are found in contact, display, and reunion contexts. Until both the terminology of vocalizations and their spectral information is made consistent and the full bandwidth of social vocalizations is obtained, these should be considered preliminary observations. The evolution of acoustic communication signals shows conservation in features and should be looked at in delphinids.

The universal features of both intra- and interspecies communication is a potential field of investigation. Morton (1977) has attempted to define the motivational and structural rules for birds and mammals. McConnel (1990) reported the cross-cultural mapping of acoustic signals and affective states in humans during communicative interactions with dogs, indicating the emergence of convergent processes of signal use. Evidence for feature conservation of affective states in human infant communication (Hauser 1996) and cross-cultural signals (Clynes 1977) have been noted, indicating that similar perceptual strategies, as far as phonetic boundaries, may be the rule not the exception. Strategies of categorizing along an acoustic continuum may be an ancient evolutionary mechanism and categories may evolve independently but consistently due to physiological mechanisms.

3.10 Social Acoustics

While psychoacoustics may be well understood (Nachtigall et al., Chapter 8), social acoustics, "the cultural encoding of information heard and its meaning," is not. The detection of conspecific fighting at a distance may include the following: broad and subtle messages, including the types of sounds associated with a particular behavior (i.e., squawks during fighting, or the subtle escalation and rate of such sounds in a sequence of activity); and general information about individuals engaged in the behavior; their geographical location, gender, or behavioral messages such as predicted outcomes from a confrontation by changes in loudness of a sound, rates of sounds, and silent periods. The potential combination of information such as hearing the squawks of a known individual, conspecific replies, the escalation of rates or intensities of vocalizations, and participation by other identifiable conspecifics might be information a receiver could potentially hear and use. This may yield decision-making information (coming to the aid or fleeing a situation) based on social status or physical abilities of the individual receiver. Spatio-temporal features may be preserved, including both the merger of time-dependent (relative spacing of signals in time) and time-independent (grammatical order and rules) cues, preserving the sequence, rhythms, time, bouts, intensity of rate or signals, and grammatical rules of communication.

Although echolocation has traditionally been thought to be used in orientation and navigation, dolphins produce a type of echo "buzzing" while playing with objects and conspecifics. *S. frontalis* often echolocate intensely while playing with relatively inanimate objects such as sea grass and sea cucumbers during conditions of excellent underwater visibility. Since such immobile objects negate the need for targeting practice, such buzzing could serve as an acoustic point or tactile stimulator rather than a tool for targeting or debilitating the object. When buzzing conspecifics, certain areas of the body are buzzed, inferring some possible rules or etiquette about the nature of social echolocation.

The relative positioning of conspecifics could facilitate the reception of ensonification information. For example, *S. frontalis* calves position themselves below the mother during foraging, traveling, and socializing, potentially maximizing exposure to the use of echolocation for both hunting and socializing. During male coalition behavior, male *S. frontalis* group within body contact, facilitating not only a potential tactile requirement for reassurance or the aquatic version of piloerection, but perhaps maximizing the group's ability to share and perceive reflected signals from the object of their sonic attention. Similar physical behavior has been observed in *S. attenuata* in tuna nets (Pryor and Kang-Shallenberger 1991). Close proximity and angle are critical in determining the eavesdropping abilities of *T. truncatus* (Xitco and Roitblat 1996) and dolphin formations and relative positions may facilitate aspects of hearing.

4. Sensory Envelopes and Potential Information

The total sensory envelope of potential information available for dolphins may include vocal as well as nonvocal signals (e.g., visual, tactile, kinesthetic, and chemoreceptive). Some of the obvious needs for hearing and deciphering information include:

1. environmental navigation and orientation
2. predator detection and alarm
3. coordinating activity
4. signals for group cohesion
5. stealth options
6. communication (short distance, long distance, and multimodal)
7. social negotiation and monitoring

Salient information is in the eye of the beholder, and relative salience will vary as a function of signal change in the environment or the social envelope (Fig. 5.2). Potential dolphin sound sets include:

1. environmental—waves, current, seismic activity, rain, boats (see review in Richardson et al. 1995)

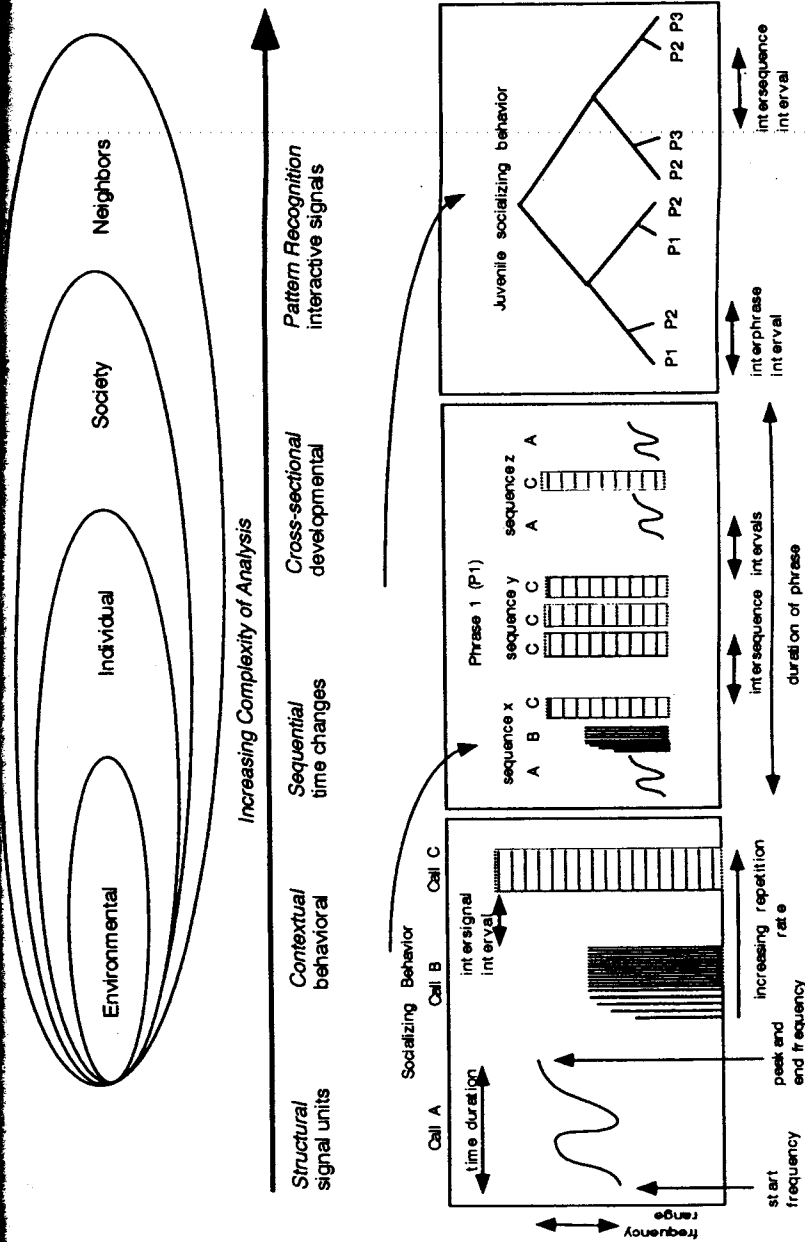


FIGURE 5.2. Acoustic sensory envelopes for an individual include exposure to environmental, intraspecific individual, intraspecific social, and interspecific neighboring sounds. With such increasing levels of acoustic information available, concomitant analysis tools need to be employed to adequately decipher patterns of those signals. An increasingly complex continuum of analysis tools, from structural units to pattern recognition, shows the relative breakdown of potential information gleaned from such techniques. See text for additional explanation.

2. the individual (intraspecific communication signals—vocal, nonvocal, nonacoustic, multimodal)
3. the society (group rules, eavesdropping, coordination of signals, sound glances, shared attention and observations, social sonar, acoustic gazing/body parts)
4. the neighbors (interspecific communication signal exchange through conservation of signals in evolution)

Traditionally, dolphins are thought to use active echolocation to obtain information from their surroundings, both during limited visibility and pursuit of a prey item. However, information is likely extracted from listening to, and making sense of, the environment, conspecifics, and neighbors. The detection, decoding, and deciphering of available signals is dependent on signal-to-noise ratio, critical ratios of hearing, "signature" or feature information from objects and movement, and developmental (physical and social) stages. It may also include more advanced concepts such as "auditory scene analysis," as discussed by Bregman (1990). Bregman argues that the auditory system builds a picture of the world through emergent perceptions of streams of information. Such streams may include information gleaned from *sequential* auditory events (such as a series of environmental sounds) or those gleaned from *simultaneous* spectral information (such as the timbre of the human voice). In either case, the auditory system may have evolved these features to order information into natural groupings that make sense in the real world. Such features are regularly found in the visual system (e.g., size and constancy). As higher-order emergent perceptual features, sequential and simultaneous processing of information should be examined in the world of delphinid audition.

Some pertinent questions around delphinid hearing might also include:

1. Does the acoustic mode kick in when vision is lost?
2. Does critical information include silence and space between sounds?
3. Is there redundancy in such a communication system, and, if so, where does it reside?
4. Does the cessation of calling increase listening and, therefore, detection abilities (signal-to-noise ratios) versus a steady-stream conspecific noise to interpret?
5. How do dolphins learn to "hear" and discriminate salient features of their environment, and are there opportunities to observe this process?

4.1 Detection, Decoding, and Deciphering

4.1.1 Detection

For complex hearing and communication, a dolphin must have the perceptual and cognitive abilities to restrict attention to things of importance in the environment and reject the rest. Increasingly complex sensory systems are able to process wide ranges of physical and social data with higher

sensitivity. Sound has an advantage as a medium for two-way, modifiable information (Norris and Evans 1988). It is unclear if dolphins use passive listening for predator detection, if they use their active echolocation system, or both. In the Bahamas, audible vocal activity ceases in murky water, counterintuitive to expectations during such conditions. Dolphins echolocate sporadically on or at objects on the bottom after apparently passive detection of information. The lack of echolocation clicks produced during traveling formations, low-light, and nocturnal feeding conditions also supports the importance of listening, and using echolocation to "follow-up" on suspect sounds. Echolocation may be a secondary, or an additional proactive, searching technique after other primary signal detection systems are employed. The questions then become: When do dolphins listen and when do they actively search? When is it safe to broadcast your signature whistle and other social sounds, and when is it smarter to listen and decode instead? These questions have been relevant in the recent studies on acoustic alarms and porpoise mortality reduction (Kraus et al. 1997) and in recent results of the significance of silence in wild bottlenose dolphins (dos Santos and Alamada 1998).

The costs of vigilance, usually by active scanning, have been calculated for other species (Illius and Fitzgibbon 1994; Shennan et al. 1994), but passive vigilance systems that listening might provide have not been addressed. Individual passive acoustic vigilance and acoustic "eavesdropping" of the vigilance activities, or flight activities of neighbors (in dolphins, sharp clicks or cracks that precede rapid fleeing) have distinct advantages over a visual or active acoustic vigilance system. Such conspicuous acoustic signals insure that information on predators passes freely from one individual to another.

The need for stealth could be critical for both a prey species and a predator. An interesting example is the recent work by Barrett-Lennard et al. (1996) on echolocation strategies by fish-eating versus mammal-eating *O. orca*. This study documents that *O. orca* use passive listening as a primary means of locating prey and use different echolocation patterns for different hunting strategies (i.e., they mask their clicks and encode their signals in background noise—acoustic crypticity—when hunting other cetaceans, prey that can hear their high-frequency clicks). In contrast, *O. orca* hunting fish do not mask their high-frequency signals for fish that do not hear in high-frequency ranges. They also found no correlation between either group size or clarity of water and increased echolocation rates, which suggests that echolocation does not directly kick in when vision fails. This suggests that passive listening may be primary and echolocation, as an active and supplementary system, is used for final targeting of prey or clarification of information that has been already detected.

Clupeid fish have recently been reported to respond to ultrasound (Mann et al. 1997) and to simulated dolphin echolocation (Mann et al. 1998), suggesting even more need for stealth hunting skills for predators of such fish. Mann and his colleagues report that all extant clupeids share this audi-

tory specialization, preceding the evolution of marine mammal hearing and sound production. Such convergent evolution, like the specialization of moths to detect ultrasonic signals of bats, may also suggest that the marine environment contains enough biological and possibly nonbiological ultrasonic signals to warrant the specialization of ultrasonic detection, possibly preceding the evolution of ultrasonic production specializations (also see Richardson et al. 1995, p. 92 for ambient ultrasonic biologicals, bubble, and thermal noise).

Dolphins are both prey and predator; prey for sharks and orcas and predators on fish and squid. Whether dolphins systematically detect ultrasonic information and low-frequency vibrations from the movement of their prey or predators, in addition to from their environment, is unmeasured but is an intriguing possibility. Although most species of dolphin are sensitive to the middle range of frequencies, many produce signals with a bimodal frequency band, emphasizing, for example, in *S. frontalis*, the 40 to 50 kHz range and another 130 to 140 kHz area (Au et al. 1998). If dolphin hearing and communication has evolved under the above pressures, then silent areas in their bandwidth production might indicate frequency bands that may be most sensitive to hearing salient cues in the environment, bandwidths detectable by prey (such as 80 kHz detection of simulated bottlenose nose clicks by shad [Mann et al. 1997]), or bands most available for active signal transmission between conspecifics.

Another interesting aspect for the detection of signals is the transmission pathway of sound through the lower jaw and body. Open-mouth behavior during agonistic encounters is certainly a postural and visual signal for many delphinids, but it has potential for the manipulation of sound or chemical reception. At first glance, this activity can look simply like the venting of an aroused dolphin, but upon further contextual observations we see open-mouth orientation when no receiver of such a visual signal is within range. Could it be that dolphins scan the water with their tongue for possible chemical cues of a conspecific? Could they be orienting their lower jaw to "tune in" and localize sounds from other dolphins in the area? (see Ketten, Chapter 2, for discussion on acoustic "windows"). "Feeling sound," or the ability for mechanoreceptors on the body to receive acoustic information, are potential senses used during the detection and decoding of environmental and conspecific sounds. Critical information exists in the low-frequency bands and includes environmental sounds, water pressure, currents, seismic activity, predator movement, and components of conspecific sounds. Although most vocalizations studied are above 2 kHz, many conspecific sounds emphasize low frequencies and most environmental noise is less than 2 kHz.

4.1.2 Decoding

Decoding signatures in the environment is critical to the initial processing of sensory information by all animals. Bats determine not only distance,

speed, and size with their echolocation, but insect echoes contain insect-specific information of the wing beat frequency, length, types, and structure, providing prey-species information (Kober 1988; von der Embe 1988). In this case, information is encoded within time intervals and changes in intensity. Could such information about prey or conspecifics be encoded in the dolphin's environment or from ensonified objects? Do dolphins hear fish buried in the bottom by their movement, and can they determine whether the fish is a preferred species or size by such signatures? Roitblat et al. (1995) present data that suggest dolphins exploit frequency and time domain information and make fine discriminations of buried objects based on high-amplitude components in signals.

The decoding of conspecific social signals is also a puzzle. Signature whistles have long been thought to contain individually specific information. Repetitive broadcasts of "signature" whistles may serve one such function. However, other possible levels of information contained in a whistle include species identity (Wang et al. 1995), family or pod dialect (Ford 1991), and emotive states (Caldwell and Caldwell 1967). Conspecifics may also use their own signature whistle to contact another member of their group. If dolphins can discriminate between the owner of a "signature" whistle and a conspecific using the same whistle, other information such as "timbre" or voice qualities, or at least contextual information about the sender, must be available. Identification features need not be limited by contour shapes of whistles, as evidenced by click codas (Watkins and Schevill 1977) and signatures contained in echolocation trains (Barrett-Lennard et al. 1996). Nor has the signature or "voice" information been seriously looked at within the diverse category of delphinid burst-pulsed vocalizations. Burst-pulsed sounds contain and modulate the same acoustic parameters utilized by individually unique rhesus monkey copulation calls (Hauser 1993). Such information may be more available to conspecifics than we realize, making the listening and hearing of a social exchange of vocalizations rich in its potential complexity of extracted information. Embedding of information may be encodable through the modulation of acoustic parameters and decodable by conspecifics, and possibly by predators.

The structural approach in determining relevant units of analysis in communication systems involves choosing between multiple acoustic parameters, including duration, amplitude, pitch, contour, and shape, and applying the appropriate analysis methods. The number of possibly relevant parameters is often infinite and undefined, but methods in hardware and software for analogous acoustic and visual signal analysis exist and have been used for a multitude of species (Clark et al. 1987; Hauser 1996).

It is critical that we begin to think about the perceiver's perspective rather than simply the production features of a signal. Subtle modulations of gross signals allow additional information to be communicated or at least detected. Modulated prosodic features such as spacing between signals can

regulate the cadence of a message that may signal an increase or decrease in vigilance or aggression, as in prairie dog vocalizations or in human narrative (Hauser 1996). Considering the above, and the individual, gender, and relational information overlaid in such signal sequences, complicated decoding such as, "My associate *X* is escalating his conflict with dolphin *Y*. I hear no other coalition partners around synchronizing their vocalizations with his, therefore my action could be to help," seems plausible during long-distance scenarios.

In human communication, both structural design features and their perceptual salience play a role in decoding human speech (Hauser 1996). Human voices convey information about objects and emotional or affective states. If voices encode information about emotional states, exposure to this information is likely used by individuals to assess social situations. The actual form of the vocalization may contain intent in its structure, as in human speech (Clynes 1977). Such stereotypic prosodic contours of affective states provide consistent information for individuals in a communicative setting. Prosodic contours provide information about affective states while referential information resides in perceptually discrete units of sound. In the human language, such aspects as "voice onset time" are critical in separating functional units of vowels and consonants. Such features can also be discriminated across species (Kuhl and Miller 1978). Since the pioneering work in primate alarm calls (Seyfarth et al. 1980), such subtle acoustic features of nonhuman animal calls have been proposed as a place where information, salient and perceivable by the species, may reside. However, methodological issues of sampling dolphin behavior in the contexts with potential referential information (feeding and predators: see Hauser 1996, p. 520) are still difficult to obtain.

If we attempt to move beyond the analysis of single calls and into sequential analysis (time-dependent modulation of parameters, or time-independent aspects of the order of signals), we begin to look at the long-term ordered relations between signal use and its determinant behavior, such as changes in arousal level or even semantic meaning. Signal relations have been discussed on theoretical grounds (Johnson 1993). The inherent assumption of the independence of signals in restricted time is limiting for signal relations analysis.

In addition, the simultaneous perception of sound is also of relevance in signal relations. Au (1993) discusses the possibility that dolphins may perceive a "time separation pitch" based on differences in highlight arrival, thus allowing a holistic perception of a sequence of sounds. This is also reported by Bregman (1990) in his discussion of auditory scene analysis by both sequential and simultaneous processing by the auditory system. Dolphins have great temporal resolving abilities (Johnson et al. 1988), and whether dolphins perceive this change as significant is unknown, but such changes in rates or differences in onset time and cessation are viable cues available to individuals (Barrett-Lennard et al. 1996).

We do not know if dolphin vocalizations are discrete, graded, or a mixture of types. When graded acoustic repertoires exist, they may still be treated as perceptually discrete because the resulting behavior itself can be a distinct decision such as to flee, fight, or terminate an interaction. Changes in pitch across a sequence of calls encodes the termination of a bout by its relationship of signals, in this case frequency over time (Hauser and Fowler 1991). A variety of acoustic parameters can be modulated to encode information (Table 5.4) including signal duration (Ehret 1992) and frequency modulation (May et al. 1989). Sophisticated and detailed analysis has also been applied to visual and facial features of human behavior (Ekman 1982).

Other potential detection cues in the production of social signals includes: (1) The directionality of sounds, which has come into question based on the directionality of echolocation clicks and the debate over continuum and mechanisms (Murray 1997). Allowing a conspecific to locate you in space would have distinct advantages in the wild. In many animal communication systems the sender of information changes source levels for different recipients and distances (Smith 1977). (2) The tactile issues of sound reception remain unresolved regarding the role of the trigeminal nerve and synesthetic qualities of perception. (3) The role of silence and listening as a cue and a mode of operation. For a discussion of the evolutionary pressures and issues of the development of communication systems see Evans and Norris (1988) and Hauser (1996).

TABLE 5.4. Examples of acoustic and visual modulation of information

Species	Type of Modulation	Modality	Examples	Reference
Macaques	Frequency	Acoustic	Downsweeps, upsweeps	May, Moody, and Stebbins 1989
Mice	Signal duration	Acoustic	Ultrasonic clicks by packets of time	Ehret 1992
Humans	Frequency Spacing Relative position	Visual	Distance between eyes Changes of features Symmetry of features	Ekman 1982

Potential parameters to be modulated in a dolphin communication system.

Type of Modulation	Modality	Examples
Frequency	Acoustics	Numbers of types of vocalizations per unit time
	Visual	Numbers of visual signals per unit time
	Tactile	Rate of rubs bouts, etc.
Amplitude/intensity	Acoustic	Source levels, changes in
	Visual/tactile	Rates of activity per unit time
Duration/spacing	Acoustic/visual	Absolute or relative time durations of signals
	Tactile	or intersignal intervals.

4.1.3 Deciphering

The deciphering of environmental and social signals is dependent on feedback from experienced individuals and direct experience of the perceiver. Pertinent to young dolphins is exposure to the milieu and repertoire of passive information and their abilities to observe the contextual reactions of their mother, siblings, and conspecifics. Although social learning has been emphasized in cultural transmission of information, higher mammals depend on exposure to a rich repertoire of signals, in multiple modalities, before production and modification of functional signals transpires.

The role of audience and feedback in categorizing relevant cues in the environment must be important during development. Generalizations about signals in the world (e.g., alarm calls and postural cues) may need to be refined and confirmed by more experienced conspecifics and may help to exemplify the meaning of signals. The importance of signal relations, not just the structure of the signal itself, form an intricate and complex web of information to filter (Johnson 1993). Escalation of behavior, relative rates, sameness or difference, strength, and timing of signals all convey important information.

Alignment of attention and shared coordination is key to the synchrony of behavior for mutual goals in dolphins including shared attention and referential pointing (Xitco 1996). Conspecifics that are within an acceptable angle and proximity to an echolocating dolphin can eavesdrop to supplement their information (Xitco and Roitblat 1996). In addition, the ability to detect salient features or essential signature information is evidenced in phantom echo experiments (Au and Moore 1988).

Evidence that dolphins may share sonar information, that they may be able to eavesdrop and infer locations of prey or conspecific behavioral activity by listening, and that they interpret echoes or social signals to maximize their information about the environment or changing social conditions all supports the potential importance of observational learning in delphinid society. How do dolphins learn to understand acoustic signals, how do they learn to produce them, and how do they learn their appropriate social use? Do socially interacting dolphins have liabilities around expressing too much information about their emotive state, identity, or status of confrontation?

5. The Development of Signals and Possible Transmission Mechanisms

After looking at the sensory envelope required to survive by adults, we can begin to see how young dolphins might begin to decipher their environment. During their lives, young *S. frontalis* are exposed to a variety of sensory signals, including acoustic, visual, and tactile, and social interactions

including group foraging, courtship, fighting, playing, and interspecific interactions. This social, sensory, and cross-generational exposure is similar to the developmental systems of primates and hominids where comprehension of the function of a communication system precedes production of the signals themselves; exposure to, and comprehension about, social interaction and language necessarily take place before production and active teaching.

What are the transmission mechanisms involved in such a learning process? Mechanisms of exposure and transfer of information include the use of observational and social learning, teaching, mimicry, synchronization of behavior, and exposure to multimodal, behavioral, and generational activities. Learning can be either vertical (information is passed between parent and offspring), oblique (passed from the parental generation—(e.g., aunts and uncles—to the young), or horizontal (passed from peer to peer within generations) (Fig. 5.3). Vertical transmission has the advantage of being conservative and retaining traditions within a society. Horizontal transmission has the advantage of being fast and dynamic, with great information exchanges possible in short periods of time, spreading possibly urgent information through a society for rapid response. Ideally, selection

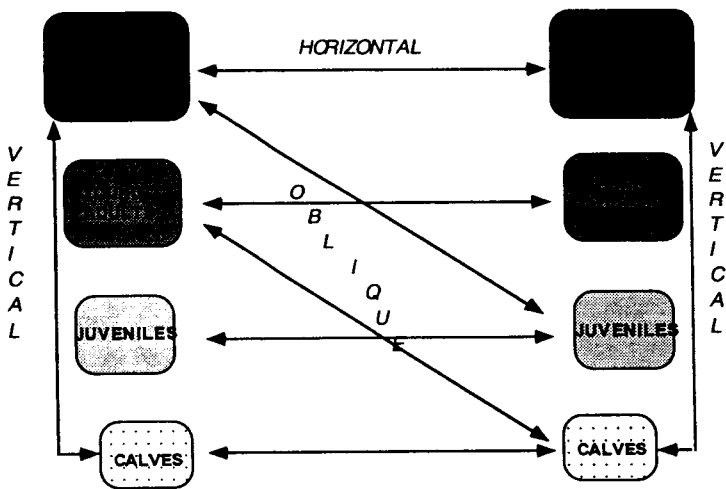


FIGURE 5.3. Transmission mechanisms for acoustic learning can vary from: (1) vertical—between parent/adult and a younger individual such as a calf; (2) horizontal—where individuals of similar age and experience pass information to each other; and (3) oblique—where information may flow between all age classes. While vertical transmission encourages the passing of traditions and is static and conservative, horizontal and oblique transmission is dynamic and fluid and encourages rapid exchanges of information between individuals. A society may show conservative transmission, dynamic transmission, or a combination of both.

might favor a combination of mechanisms, that is, a highly horizontal culture would favor rapid adaptations with some stabilizing reality checks of vertical learning such as time-honored, tested, and proven traditions. Social learning would permit rapid evolution (e.g., faster than genetic changes for mate selection). Oblique transmission is also conducive to utilizing the repository of experience and information available from older, more experienced individuals in the society.

As we increase our abilities to gain finer detailed information about age class, gender, individuals, and relationships in a society, we increase our ability to understand what information is available. Developmental aspects of categorizing sounds have been documented for primates (Seyfarth and Cheney 1980) and other terrestrial species. It is likely that such insight into delphinid societies will yield similarly valuable information. Comprehension of cultural information is thought to be primary to production (Savage-Rumbaugh et al. 1986). Developmental emphasis on exposure to listening and feedback of appropriate behavior may be important in a society, that is, production may occur only when an individual is required by circumstance to lead or communicate an action or intention.

An extended maturational period of development, the period of both physical and social weaning before sexual maturity, may serve as a time to refine the decoding of social signals. The focus of juvenile activity beyond the basic survival issues of foraging, includes play, a high-risk activity yet one that is acceptable in adult circles and carries a meta-message of signal use. Societies with cross-generational or even cross-species access to transfer of information are well suited for learning. In many species of open-ocean delphinids, age classes overlap on a regular basis and in some, mixed species aggregations are common. In the Bahamas, a complex relationship between *T. truncatus* and *S. frontalis* extends the exposure to cross-species communication signals. Mimicry, both vocal (Richards et al. 1984) and postural (Xitco 1988; Herzing 1996) has been documented and is a likely mechanism for transmission and learning. Dolphins are reported to hear human vocalizations above water and adapt and extend their own species signals to humans (Pryor 1986). Complex informational exchange between species, including aggression and cooperation, is likely with sympatric species exposure at a young age (Herzing and Johnson 1997).

How might dolphin hearing be intertwined with such transmission mechanisms? Young dolphins must be able to detect, decode, and decipher signals from the environment in order to react appropriately, both physically and socially. In social contexts it may be difficult for us to observe signal use and its associated circumstances and behavior. Messages (vocal, visual, and tactile) can be *nonbehavioral*, such as age, location in space, and identification, or *behavioral*, which allows prediction of social outcomes or impending behavior (proximal or long-distance). Messages can also be *broad*, signaling a general state of arousal by posture or types of signals, or *subtle*, where encoded information is specific to an individual's state by such

measurable structural features as duration of a signal, amplitude, changes in rate of delivery, shifts in frequency, or relational features of signals (a signal may be merely louder or longer than the previous one). Prosodic or rhythmic features of communication are critical for broad activity, but can also contain subtle identity information of the escalation of impending behavioral changes. A human observer in the water may, at a distance, hear a combination of types of signals that may indicate the general state of activity (e.g., fighting, foraging). If the level of general activity (Herzing, unpublished data), and the diversity of sounds present and audible distances of up to 2 km (dos Santos et al. 1995) can be obtained by a listening human, then dolphin decoding must contain much more complicated levels of analyses. Potentially contained within conspecific signals are individual identifiers, emotive information, and other changes in behavioral states, possibly discernible to the experienced dolphin who has previously observed, interacted, and participated in conflict resolution.

6. Special Cases of Communication

A review of the sensory and cognitive literature of dolphins reveals that their capabilities may include the following:

1. Cross-modal perception: intermodal transfer of information is relevant when dolphins synchronously generate visual images from audition signals and the reverse. Pack and Herman (1995) report that dolphins recognized complex shapes across the visual and acoustic sense. Similar cross-modal results have been obtained by Azzali et al. (1995). However, an alternative interpretation to cross-modal representation has been discussed (Popper et al. 1997).

2. Feature detection and filtering to provide minimal information (Herman et al. 1990).

3. The presence and absence of objects, comprehension of syntactical rules, and two-dimensional representations in space of abstract television images and time displacement (Herman et al. 1990).

4. Shared listening and eavesdropping: the ability to eavesdrop and glean information through the return echoes of conspecifics (Xitco and Roitblat 1996), also termed "interception" in fish communication (Myrberg 1981). Although the distance and position to the source of the active echolocation clicks is critical, this provides some suggestion that dolphins may have the ability to share information as a group.

5. Signature decoding may be unique enough to extract pertinent features (Au and Moore 1988).

6. Synchrony, imitation, and mimicry (Xitco 1988).

Support for the application of these capabilities of dolphins in the wild include: the ability to encode, store, and retrieve information including indi-

vidual, pod, and species recognition through signature whistles, dialect, or species whistles; short- and long-term memory abilities, inference about the function of signature whistles, and the need for individual recognition within the group in order to sustain long-term relationships; and the application of flexible modeling systems in their conspecific and allospecific behavior through mimicry, imitation, coordination, and synchrony of behavior.

Although there is no existing evidence for the use of referential signals by dolphins in the wild, as has been observed for primates (Cheney and Seyfarth 1982), experimentally dolphins utilize a "point" system for drawing attention to an object with a human observer present (Xitco 1996). Although unique to the human audience, this may suggest that dolphins utilize another system of pointing, possibly through their focused echolocation beam, to draw and share attention to an object. The utilization of their whole body as a point may also be another way of drawing attention to a specific object or referent. The evolutionary pressure should be great for maximizing information of individuals and subsequently relaying it back to the group. Attaining samples of referential signal use in appropriate behavioral contexts, such as sounding the alarm about specific predators, or announcing discovery of food sources as has been described for terrestrial species (Hauser 1996), may be difficult in the aquatic environment.

Rhythms and prosodic features may be important in the encoding and decoding of language (Simmons and Baltaxe 1975). Both rhythm and body motion are often in synchrony with emotional states, and rhythmic acoustic exchanges occur between many animals. Mimicry has been documented to be critical in both intra- and interspecies communication (Richards et al. 1984; Xitco 1988). Biological entrainment (the natural tendency for communication signals, including nerve pulses, pheromones, and social behavior to display contagion), is a feature both of the basic mammalian nervous system and of higher social and interactive systems (Raloff 1996).

Concomitantly, movement and postures may serve to not only supplement but break up acoustic utterances into units, analogous to highly refined codes such as human utterances that form consonants and break up glottal vowel codes into various units (Savage-Rumbaugh 1994). Aspects such as voice onset are critical parameters in human speech. Consonants, which are basically short clicks and hisses, act as boundaries around vowels, allowing us to perceive discrete categories or phonetic units. Both non-human and human animals have evolved to hear clicks and hisses as environmental information, utilizing longer vowel-like sounds for communication. Even though auditory systems have evolved different ways of listening, universal acoustic features including sharp onset times, fundamental frequency use, and prosodic elements of rhythm and space show evolutionary continuity between species.

7. Areas of Future Inquiry—Acquisition, Analysis, and Application

Future areas of inquiry and examples of the benefits gained from each technique are listed in Table 5.5 and include the following:

7.1 *Sensory and Social Sets of Information*

7.1.1 Environmental Envelopes

Environmental envelopes, including the sounds of wind, waves, and fish movement, need to be assessed (see Richardson et al. 1995 for review).

What does a fish moving under the sand sound like? What transmits during long-distance conspecific information (i.e., frequency, rhythm, escalation of vocalizations)?

7.1.2 Context, Development, and Identification of the Individual Vocalizer

Correlating vocalizations with behavior is critical, even if done only from a surface perspective. The importance of including contextual information, including individuals, audience, and relationship, during the use of communicative signals has been emphasized by many researchers (Smith 1977; Tavolga 1983). Learning, memory, development, and the relationship between cognition and communication is relevant to delphinid communication (Johnson 1993).

7.1.3 Abilities to Detect, Decipher, and Discriminate the World

Recent work on language in nonhuman species focuses on aspects of receptive competencies including listening, understanding, and comprehension as primary to functional testing of a communication system (Savage-Rumbaugh et al. 1986; Herman and Morrel-Samuels 1996). Sound sets available to dolphins determine their ability and need to decipher signals for environmental navigation, predator detection, and social negotiations.

7.1.4 Measuring Affective States

In addition to providing sociological and ecological parameters that are external to the vocalizer, both direct (physiological) and indirect (postures, movements) measures can be integrated into analysis of affective states and correlated acoustics of individual dolphins.

7.1.5 Full Bandwidth Recording

Bandwidth-limited technology has been the largest obstacle in obtaining full sound production information. Our inability to regularly document the

TABLE 5.5. Future areas of inquiry: techniques and benefits

Type of Inquiry	Techniques Used	Benefits/Information Gained	Examples of Work
Sound sets	Catalog of environmental and conspecific sounds	Addresses what potential information is available to hear	Richardson et al. 1995
Structural	Parametric measurements of signal structure	Physical aspects of sounds heard	Morton 1977; Wang et al. 1995
Contextual	Behavioral correlates to life history and behavior	Variations by behavioral changes	Herzing 1996
Individual/longitudinal	Individual vocalizations categorized/analyzed	Individual variations and development of hearing and sound production	Sayigh et al. 1990
Sequential analysis	Order of sounds and their probability of presence	Preserves spatio-temporal features of communication	Stooten 1994; van Hooff 1982
Cross-sectional	Analysis of age class uses of sound and hearing	Preserves physical and behavioral changes of hearing	Seyfarth and Cheney 1980
Perceptual categories	Experiment and natural analysis of salient features of sound	Defines categories of significance in multiple parameters	May, Moody, and Stebbins 1989
Phantom echoes	Detection and analysis of "signature" features available	Defines minimum information and type available in environment	Au and Moore 1988
Neural networks	Advanced pattern recognition on multiple dimensions	Defines greater information available and closer to brain processes	Magnusson 1996

high-frequency information available to social species greatly hinders us from observing the full spectrum of information. With the development of high-speed digitizing equipment and its application in the field, our abilities to document the full acoustic repertoire of signals should increase.

7.1.6 The Directionality of Sound and Its Use

Determining the directionality of social sounds (burst-pulsed and whistles) as well as the directionality and use of dolphin echolocation as a potential "point" for conspecifics would be useful. In addition, the angle and proximity required to successfully eavesdrop on returning echoes in the wild would greatly illuminate signal use.

7.2 *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 (1) the pulsed versus continuous nature of sounds, and (2) 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 nonhuman primates (Struhsaker 1967; Cleveland and Snowdon 1982), avian repertoires (Marler 1982), and bats (Gould 1983) and needs to be explored in delphinids.

7.3 *Graded or Discrete Signals, Signal Relations and Prosodic Aspects of Sound*

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 in which prosodic features of sound, including rhythm, silence, and intensity, communicate information. Gish (1979) analyzed the temporal relationship of sounds between two *T. truncatus* 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.

These frameworks suggest that analyzing discrete and graded multimodal signals, the rhythm and sequence of signals, and social elements that form a context for the animal in an environment play a crucial role in the interpretation of communication systems of many animals, including delphinids. The universal aspects of the evolution of communication signals may also be potentially elucidated by this area of inquiry.

7.4 *Cross-Modal and Synesthetic Work*

Many communication systems are graded on multiple dimensions, not only acoustic or single-mode, but across modalities as in the tactile and visual modalities of humans, although other cross-senses exist (Marks 1978). The successful use of language in both the visual and acoustic modalities, combined with the temporal analysis abilities of the dolphin brain, may reflect on the integration of temporal patterns within the dolphins "*Umwelt*."

In addition to the visual and acoustic intermodal transfer, an intriguing area for intermodal research is the tactile modality, given the size and position of the trigeminal nerve in the dolphin (Morgane and Jacobs 1972; Schusterman 1990). Human cross-modal work has included perceptions of size, form, space, time, and the coding of perceptual information (Marks 1978). Cross-modal translation may be ideal for reducing the processing load of a characteristic set of information about the environment, object, or conspecifics. Such perception may have to do with signatures of essential information that are modulated in many dimensions. Sentic states (Clynes 1977) and dimensions of affect have been described for human infant communication (Hauser 1996) including contour-specific features for approval, attention, comfort, and prohibition. This indicates that the production and perception of forms in time are modulated by emotive information, often synesthetically by nervous system physiologic codes created by sound, movement, and touch.

7.5 *Advanced Analysis—Sequential, Signal Relations, and Pattern Recognition*

Although traditional behavioral sampling is often used in the study of delphinid communication (Altmann 1974; Slooten 1994), a neglected area of analysis is in the rhythmic and sequential aspects of behavior and acoustics (van Hooff 1982). Signal relations in a sequence of action may be worthy of exploration. For example, the relative amplitude in a call or the intensity or rate of a postural movement can add information to a sequence of events critical for the receiver to interpret. The frequency of a signal, the rhythm, silent pauses, differences in parameter as such as frequency or amplitude modulation, and the sequential escalation of signals are higher-level communicative features for accessing both social negotiation and passive informational content. Sequential analysis has been used in human communication and yields both time-dependent (rhythm) and time-independent (grammar/order) aspects of communication combined into innovative pattern recognition programs (Magnusson 1996). Sequential analysis means that the order and temporal integrity of signals are conserved in space and time.

The recognition of rhythmic components in dolphin communication has been documented by both Lilly (1965) and Gish (1979). Both studies refer

to specific mimicry of space between signals and initiation of signals. Signal relations are of ultimate importance in many animal communication systems, and initial work on amplitude discrimination has been conducted (Burdin et al. 1973; Vel'min and Dubrovskii 1978) indicating discrimination in amplitude features of signals. Preliminary recognition of sequential patterns of tones with durations or intersound intervals greater than 2s were not reliable (Ralston and Herman 1989).

The pattern recognition of rhythm, graded signals, sequential information, cross-modal signals, escalation in rates and intensity of signal over time, and signal relations are needed to fully understand delphinid hearing. New pattern recognition and neural network techniques (Murray 1997; Deecke et al. 1999) and the possible gradation of parametric continuums provides one of the most productive ways to analyze critical parameters. It has even been suggested that production of sound (with increased click rate turning into whistles) is a continuum, behaviorally and structurally. These lines of inquiry may allow eventual comparison between behavioral states, age, and species.

7.6 Shared Cognition—Cross-species, Eavesdropping, and Phantom Echoes

Signals evolve by virtue of their being detected, decoded, and responded to differentially by conspecifics and, perhaps, neighbors. Signal evolution is influenced by interspecific audiences and their discriminative abilities, especially in sympatric species (Smuts et al. 1987; Herzing and Johnson 1997). Shared cognitive environments take on a type of relevance for sharing communication and negotiating. Mutual cognitive environments between species are likely to produce pressures for interspecific communication skills and signals. The acquisition and coopting of signals and of detection abilities is critical in understanding the evolution of communication signals and hearing. Sentinel species give alarm calls either to warn mixed species aggregations of approaching predators (Munn 1986), or to effectively deceive or divert a competitor from a desired goal, thereby involving the coordination of different cognitive environments. Evolutionarily there should be a high value on the interpreter needing to correctly identify relevant cues from both conspecifics and allospecifics, and stereotypy and redundancy are both ways to reduce demands on such cognitive challenges.

Concomitant aspects of hearing involve eavesdropping and interpretation of minimal information. Signal deciphering through eavesdropping from conspecifics would suggest that much information is available, conspecifically, from listening and overhearing partial signals (Xitco and Roitblatt 1996). Combined with specific signature features of ensonified objects or with phantom echoes (Au and Moore 1988), this may allow complex discrimination of conspecific signals.

7.7 *Processing and Decoding of the Informational Content of Signals*

We have not decoded potential modulated information in many of the bands of frequencies in use by dolphins during social interaction. Dolphins have the ability to independently modulate acoustic parameters of their echolocation signals including click rate, frequency, and amplitude (Moore and Pawloski 1990). Our abilities to decode this information may lead to a better understanding of hearing abilities. Such modulation would likely be found, and would be worthy of analysis, in communicative signals to conspecifics, including not only frequency-modulated whistles but the potentially rich source of information embedded in burst-pulsed vocalizations. The mechanism by which such information is transmitted, shared, and modified leads us to look for examples of teaching and how a developing individual is guided and redirected toward appropriate modification of signal use utilizing the constraints of communication and hearing.

Other potential techniques to apply to dolphin sound analysis include (1) acoustic multiplexing (defined in human terms as the ability to hear conversations, background noise, and also carry on a conversation); (2) multi-mode imaging sonar (which does not use time-differential information but rather spectral information as object moves in water, thereby analyzing from the spectral signal itself); and (3) back-scatter illumination techniques developed by Buckingham et al. (1996). Given the dolphins' noisy and complex acoustic environment, these techniques would be useful to determine features of both dolphin hearing and communication. The larger issues discussed by Bregman (1990) around the perception of an "auditory scene" or unit of salient information should also be explored.

Other potential sources of subtle cues in the aquatic environment available to dolphins might include the reception of sound from molecular or physical aspects of water manipulation, such as (1) the ability to create and manipulate vortices (Marten et al. 1996), (2) the near-field effects of sound and water molecules such as heat transfer via ensonification, low-frequency particle motion, and pressure fluctuations (Turl 1993), or physical patterns set up in water molecules as described in the physics of cymatics (Jenny 1974); and (3) interference patterns from return echoes theoretically exploited for image processing by bats (Simmons et al. 1996). All hold out interesting physical possibilities of information transfer and subtle detection abilities yet unexplored.

7.8 *Standardizing, Enhancing, and Synthesizing*

Improved understanding about dolphin hearing and communication signal detection and decoding can also be enhanced by the following:

7.8.1 Standardize Terminology and Techniques

Sounds presented with both time and frequency information and power spectra (Busnel and Dzedic 1966) would be helpful. In addition, different sampling rates and equipment can alter signal form analysis (Watkins 1967) and clarification about methodologies needs to be made to avoid confusion around the terminology of vocalizations.

7.8.2 Determine Perceptually Salient Features of Vocalizations

Increased understanding of mechanistic and perceptual classification is needed to determine the natural boundaries of signal classification by delphinids.

7.8.3 Enhance the Descriptive Process of Behavior

Descriptive science is often underplayed for its value in understanding behavior. Calls with indirect (behavioral postures) or direct (physiological) measures of the caller's affective state are good independent measures of fear, distress, etc. and are critical to help refine the natural boundaries of conspecific signals. Techniques to understand fundamental units of communication, both affective and referential, and their relationship with each other may increase our abilities to extract meaning from very subtle vocal and nonvocal signals.

7.8.4 Think About Multimodal, Interdisciplinary, and Symbolic Possibilities

Thinking in broader terms of what and how information may be available to dolphins may open up some fundamental possibilities of extracting the meaning of acoustic signaling. For example, primate predator calls were first recognized as different but thought to represent levels of threat to an individual. Thinking in symbolic and referential possibilities opens up potential analysis for higher levels of information content in nonhuman species.

8. Summary

Despite recent efforts to understand both dolphin hearing and the use of conspecific signals, little progress has been made. Major obstacles include (1) regular access to dolphins, both underwater and in their natural social settings; (2) full sensory and signal recording by researchers, including both full bandwidth acoustic recordings and visual/tactile signals; (3) a lack of understanding about modulated features of dolphin social communication signals, including frequency, amplitude, and duration parameters, both

acoustic and nonacoustic; and (4) standardization of equipment, analysis, and descriptive techniques, including sufficient acoustic information, terminology, and comparative studies.

Despite these problems in the acquisition and analysis of dolphin social signals and hearing from the dolphin's perspective, anatomical, physiological, psychoacoustic, and cognitive studies lend evidence and potential direction to future research areas. In addition, new computer and analytical techniques can improve our abilities to productively and accurately decipher conspecific social sounds and their salient features.

Psychological, acoustic, and behavioral data indicate that dolphins have spatio-temporal abilities matching both their environmental and social challenges in the aquatic environment, and these abilities are reflected in the characteristics of their social sounds. Overlaid with abilities to detect, decode, and decipher sound, are the dolphins' ability to modify, mimic, and utilize complex cognitive strategies to decipher and interpret their environment, all adding to the complexity of understanding delphinid hearing.

References

- Altmann J (1974) Observational study of behavior: sampling methods. *Behaviour* 49:227-267.
- Au WWL (1993) *The Sonar of Dolphins*. New York: Springer-Verlag.
- Au WWL, Moore PWB (1988) The perception of complex echoes by an echolocating dolphin. In: Nachtigall PE, Moore PWB (eds) *Animal Sonar—Processes and Performance*. New York and London: Plenum Press, pp. 295-299.
- Au WWL, Floyd RW, Haun JE (1978) Propagation of Atlantic bottlenose dolphin echolocation signals. *J Acoust Soc Am* 64:411-412.
- Au WWL, Herzing DL, Aubauer R (1998) Real-time measurement of the echolocation signals of wild dolphins using a 4-hydrophone array. *Proceedings of the World Marine Mammal Science Conference, Monaco, 1998*.
- Azzali B, Manzini A, Buracchi G (1995) Acoustic recognition by a dolphin of shapes. In: Kastelein RA, Thomas JA, Nachtigall PE (eds) *Sensory Systems of Aquatic Mammals*. Woerden, The Netherlands: De Spil, pp. 137-156.
- Barrett-Lennard LG, Ford JKB, Heise KA (1996) The mixed blessing of echolocation: differences in sonar use by fish-eating and mammal-eating killer whales. *Anim Behav* 51:553-565.
- Bregman AS (1990) *Auditory Scene Analysis: The Perceptual Organization of Sound*. Cambridge, MA: MIT Press.
- Brownlee SM, Norris KS (1994) The acoustic domain. In: Norris KS, Würsig B, Wells RS, Würsig M (eds) *The Hawaiian Spinner Dolphin*. Berkeley: University of California Press, pp. 161-185.
- Buckingham MJ, Potter JR, Epifanio CL (1996) Seeing in the ocean with background noise. *Sci Am* 272:86-90.
- Bullock TH, Ridgway SH (1972) Evoked potentials in the central auditory system of alert porpoises to their own and artificial sounds. *J Neurobiol* 3:79-99.

- Bullock TH, Grinnel AD, Ikezono E, Kameda K, Katsuki K, Nomoto M, Sato O, Suga N, Yanagisawa K (1968) Electrophysiological studies of central auditory mechanisms in cetaceans. *Z Vergl Physiol* 59:117-156.
- Burdin VI, Markov VI, Reznik AM, Skorniyakov VM, Chupakiv AG (1973) Ability of *Tursiops truncatus* Ponticus Barabasch to distinguish a useful signal against a noise background. In: Chapskii KK, Sokolov VE (eds) *Morphology and Ecology of Marine Mammals*. New York: John Wiley & Sons, pp. 162-168.
- Busnel RG, Dziedzic A (1966) Acoustic signals of the pilot whale *Globicephala melaena* and of the porpoises *Delphinus delphis* and *Phocoena phocoena*. In: Norris KS (ed) *Whales, Dolphins and Porpoise*. Berkeley: University of California Press, pp. 607-648.
- Caldwell DK, Caldwell MC (1966) Observations on the distribution, coloration, behavior and audible sound production of the spotted dolphin, *Stenella plagiodon*. *Contrib Sci* 104:1-28.
- Caldwell DK, Caldwell MC (1971) Underwater pulsed sounds produced by captive spotted dolphins, *Stenella plagiodon*. *Cetology* 1:1-7.
- Caldwell MC, Caldwell DK (1965) Individualized whistle contours in bottlenose dolphins (*Tursiops truncatus*). *Nature* 207:434-435.
- Caldwell MC, Caldwell DK (1967) Intraspecific transfer of information via the pulsed sound in captive odontocete cetaceans. In: Busnel RG (ed) *Animal Sonar Systems, Biology and Bionics*. Jouy-en-Josas, France: Laboratoire de Physiologie Acoustique, pp. 879-936.
- Caldwell MC, Haugen RM, Caldwell DK (1962) High-energy sound associated with fright in the dolphin. *Science* 138:907-908.
- Caldwell MC, Caldwell DK, Evans WE (1966) Sounds and behavior of captive Amazon freshwater dolphins, *Inia geoffrensis*. *Contrib Sci* 108:1-24.
- Caldwell MC, Caldwell DK, Miller JF (1973) Statistical evidence for individual signature whistles in the spotted dolphin, *Stenella plagiodon*. *Cetology* 16:1-21.
- Caldwell MC, Caldwell DK, Tyack PL (1990) Review of the signature whistle hypothesis for the Atlantic bottlenose dolphin. In: Leatherwood S, Reeves RR (eds) *The Bottlenose Dolphin*. San Diego: Academic Press, pp. 199-233.
- Cheney DL, Seyfarth RM (1982) How vervet monkeys perceive their grunts: field playback experiments. *Anim Behav* 30:739-751.
- Clark C, Marler P, Beeman K (1987) Quantitative analysis of animal vocal phonology: an application to swamp sparrow song. *Ethology* 76:101-115.
- Cleveland J, Snowdon CT (1982) Complex vocal repertoire of the adult cotton-top tamarin (*Saguinus oedipus oedipus*). *Z Tierpsychol* 58:231-268.
- Clynes M (1977) *Sentics: The Touch of Emotion*. New York: Anchor Press.
- Connor RC, Smolker RA (1996) "Pop" goes the dolphins: a vocalization male bottlenose dolphins produce during consortships. *Behaviour* 133:643-662.
- Connor RC, Smolker RA, Richards AF (1992) Two levels of alliance formation among male bottlenose dolphins (*Tursiops* sp.). *Proc Natl Acad Sci USA* 89:987-990.
- Cranford TW, Amundin M, Norris KS (1996) Functional morphology and homology in the odontocete nasal complex: implications for sound generation. *J Morphol* 228:223-285.
- Dawson SM (1991) Clicks and communication: the behavioural and social contexts of Hector's dolphin vocalizations. *Ethology* 84:265-276.

- Deecke VB, Ford JKB, Spong P (1999) Quantifying complex patterns of bioacoustic variation: Use of a neural network to compare killer whale (*Orcinus orca*) dialects. *J Acoust Soc Am* 105:2499–2507.
- dos Santos ME, Alamada VC (1998) Acoustic emissions and activity patterns in bottlenose dolphins. Proceedings of the World Marine Mammal Science Conference, Monaco, 1998.
- dos Santos ME, Lacerda M (1987) Preliminary observation of the bottlenose dolphin (*Tursiops truncatus*) in the Sado estuary (Portugal.). *Aquat Mamm* 13:65–80.
- dos Santos ME, Caporin G, Moreira HO, Ferreira AJ, Coelho JLB (1990) Acoustic behavior in a local population of bottlenose dolphins. In: Thomas JA, Kastelein RA (eds) *Sensory Abilities of Cetaceans*. New York: Plenum Press, pp. 585–598.
- dos Santos ME, Ferreira AJ, Harzen S (1995) Rhythmic sound sequences emitted by aroused bottlenose dolphins in the Sado estuary, Portugal. In: Thomas JA, Kastelein RA, Nachtigal PE (eds) *Sensory Abilities of Cetaceans*. Woerden, The Netherlands: De Spil, pp. 325–334.
- Dreher JJ, Evans WE (1964) Cetacean communication. In: Tavolga WN (ed) *Marine Bioacoustics*. Oxford: Pergamon Press, pp. 373–399.
- Driscoll AD (1995) Categorizing the whistles and choruses of Hawaiian spinner dolphins. Ph.D. Dissertation. University of California, Santa Cruz, CA.
- Dudzinski KM, Clark CW, Würsig B (1995) Mobile video/acoustic system for simultaneous underwater recording of dolphin interactions. *Aquat Mamm* 21:187–193.
- Ehret G (1992) Categorical perception of mouse-pup ultrasounds in the temporal domain. *Anim Behav* 43:409–416.
- Ekman P (1982) Methods for measuring facial action. In: Scherer KR, Ekman P (eds) *Handbook of Methods in Nonverbal Behavior Research*. New York: Cambridge University Press, pp. 45–135.
- Estes RD, Goddard J (1967) Prey selection and hunting behavior of the African wild dog. *J Wildl Manage* 31:52–70.
- Evans EC, Norris KS (1988) On the evolution of acoustic communication systems in vertebrates. Part I: Historical aspects. In: Nachtigal PE, Moore PWB (eds) *Animal Sonar—Processes and Performance*. New York and London: Plenum Press, pp. 655–670.
- Evans WE (1966) Vocalizations among marine mammals. *Marine Bioacoustics*, Vol. 2. Oxford: Pergamon Press, pp. 159–185.
- Fagan R (1981) *Animal Play Behavior*. New York: Oxford University Press.
- 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*. July 1982.
- Ford JB (1991) Vocal traditions among resident killer whales (*Orcinus orca*) in coastal waters of British Columbia. *Can J Zool* 69:1454–1483.
- Ford JKB, Fisher HD (1978) Underwater acoustic signals of the narwhal (*Monodon monoceros*). *Can J Zool* 56:552–560.
- Ford JKB, Fisher HD (1983) Group-specific dialects of killer whales (*Orcinus orca*) in British Columbia. In: Payne R (ed) *Communication and Behavior of Whales*. Boulder, CO: Westview Press, pp. 129–161.

- Gish SL (1979) Quantitative description of two-way acoustic communication between captive Atlantic bottlenose dolphins (*Tursiops truncatus montagu*). Doctoral Dissertation, University of California, Santa Cruz, CA.
- Gould E (1983) Mechanisms of mammalian auditory communication. In: Eisenberg JF, Kleiman DG (eds) *Advances in the Study of Mammalian Behavior*. Special Publication of the American Society of Mammalogy 7, pp. 265-342.
- Hauser MD (1993) The evolution of nonhuman primate vocalization: effects of phylogeny, body weight and motivational state. *Am Nat* 142:528-542.
- Hauser MD (1996) *The Evolution of Communication*. Cambridge: MIT Press.
- Hauser M, Fowler C (1991) Declination in fundamental frequency is not unique to human speech: evidence from non-human primates. *J Acoust Soc Am* 91:363-369.
- Herman LM, Morrel-Samuels P (1996) Knowledge acquisition and asymmetry between language comprehension and production: dolphins and apes as general models for animals. In: Bekoff M, Jamieson D (eds) *Readings in Animal Cognition*. Cambridge: MIT Press, pp. 289-306.
- Herman LM, Tavolga WN (1980) Communication systems of cetaceans. In: Herman LM (ed) *Cetacean Behavior: Mechanisms and Function*. New York: John Wiley & Sons, pp. 149-197.
- Herman LM, Morrel-Samuels P, Pack AA (1990) Bottlenosed dolphin and human recognition of veridical and degraded video displays of an artificial gestural language. *J Exp Psychol* 119:215-230.
- Herzing DL (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, San Francisco, CA.
- Herzing DL (1996) Underwater behavioral observations and associated vocalizations of free-ranging Atlantic spotted dolphins, *Stenella frontalis*, and bottlenose dolphins, *Tursiops truncatus*. *Aquat Mamm* 22:61-79.
- Herzing DL (1997) The natural history of free-ranging Atlantic spotted dolphins (*Stenella frontalis*): age classes, color phases and female reproduction. *Mar Mamm Sci* 13:40-59.
- Herzing DL, Johnson CJ (1997) Interspecific interactions between Atlantic spotted dolphins (*Stenella frontalis*) and bottlenose dolphins (*Tursiops truncatus*) in the Bahamas, 1985-1995. *Aquat Mamm* 23:85-99.
- Hoese HD (1971) Dolphin feeding out of water in a salt marsh. *J Mamm* 52:222-223.
- Hult RW (1982) Another function of echolocation for bottlenose dolphins. *Cetology* 47:1-7.
- Illius AW, Fitzgibbon C (1994) Costs of vigilance in foraging ungulates. *Anim Behav* 47:481-484.
- Jenny H (1974) *Cymatics: Wave Phenomena, Vibrational Effects, Harmonic Oscillations with Their Structure, Kinetics and Dynamics*, Vol. 2. Basel, Switzerland: Basilius Press.
- Johnson CM (1993) Animal communication by way of coordinated cognitive systems. In: Bateson PPG, Klopfer PH, Thompson NS (eds) *Perspectives in Ethology*. New York: Plenum Press, pp. 187-205.
- Johnson CM, Herzing DL (1991) The social use of the tactile effects of dolphin vocalizations. Ninth Biennial Conference on the Biology of Marine Mammals, Dec. 5-9 1991, Chicago, IL, p. 36.

- Johnson RA, Moore PWB, Stoermer MW, Pawloski JL, Anderson LC (1988) Temporal order discrimination within the dolphin critical interval. In: Nachtigall PE, Moore PWB (eds) *Animal Sonar: Processes and Performance*. New York: Plenum Press, pp. 317–333.
- Kober R (1988) Echoes of fluttering insects. In: Nachtigall PE, Moore PWB (eds) *Animal Sonar: Processes and Performance*. New York: Plenum Press, pp. 477–481.
- Kraus SD, Read AJ, Solow A, Baldwin K, Spradlin T, Anderson E, Williamson J (1997) Acoustic alarms reduce porpoise mortality. *Nature* 388:525.
- Kuhl PK, Miller JF (1978) Speech perception by the chinchilla: identification function for synthetic VOT stimuli. *J Acoust Soc Am* 63:905–917.
- Lammers M, Au WWL (1997) Broadband recording of free-ranging delphinid social acoustic signals. Symposium of Information Processing, Vallejo, CA, 1997.
- Lilly JC (1965) Vocal mimicry in *Tursiops*. Ability to match numbers and durations of human vocal bursts. *Science* 147:300–301.
- Lilly JC, Miller AM (1961) Vocal exchanges between dolphins. *Science* 134:1873–1876.
- Magnusson MS (1996) Hidden real-time patterns in intra and inter-individual behavior: description and detection. *Eur J Psych Assess* 12:112–123.
- Mann DA, Lu Z, Popper AN (1997) A clupeid fish can detect ultrasound. *Nature* 389:341.
- Mann DA, Lu Z, Hastings MC, Popper AN (1998) Detection of ultrasonic tones and simulated dolphin echolocation clicks by a teleost fish, the American shad (*Alosa sapidissima*). *J Acoust Soc Am* 104:562–568.
- Marler PR (1982) Avian and primate communication: the problem of natural categories. *Neurosc Biobehav Rev* 6:87–92.
- Marks LE (1978) *The Unity of the Senses: Interrelations Among the Modalities*. New York: Academic Press.
- Marten K, Norris KS, Moore PWB, Englund KA (1988) Loud impulse sounds in odontocete predation and social behavior. In: Nachtigall PE, Moore PWB (eds) *Animal Sonar: Processes and Performance*. New York: Plenum Press, pp. 567–579.
- Marten K, Shariff K, Psarakos S (1996) Ring bubbles of dolphins. *Sci Am* 275:82–87.
- May B, Moody DB, Stebbins WC (1989) Categorical perception of conspecific communication sounds by Japanese macaques, *Macaca fuscata*. *J Acoust Soc Am* 85:837–847.
- McConnell PB (1990) Acoustic structure and receiver response in domestic dogs, *Canis familiaris*. *Anim Behav* 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. *Zool Biol* 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.
- Moore PWB, Pawloski DA (1990) Investigations on the control of echolocation pulses in the dolphin (*Tursiops truncatus*). In: Thomas JA, Kastelein RA (eds) *Sensory Abilities of Cetaceans*. New York: Plenum Press, pp. 305–316.
- Morgane PJ, Jacobs MS (1972) Comparative anatomy of the cetacean nervous system. In: Harrison JR (ed) *Functional Anatomy of Marine Mammals, Vol 1*. New York: Academic Press, pp. 117–244.

- Morton ES (1977) On the occurrence and significance of motivation—structural rules in some bird and mammal sounds. *Am Nat* 111:855–869.
- Murray SO (1997) The graded structure and neural network classification of false killer whale (*Pseudorca crassidens*) vocalizations. Masters Thesis. University of Hawaii, Honolulu, HI.
- Munn CA (1986) The deceptive use of alarm calls by sentinel species in mixed-species flocks of neotropical birds. In: Mitchell RW, Thompson NS (eds) *Deception: Perspectives on Human and Nonhuman Deceit*. Albany: State University of New York Press, pp. 169–176.
- Myrberg AA Jr (1981) Sound communication and interception in fishes. In: Tavolga WN, Popper AN, Fay RR (eds) *Hearing and Sound Communication in Fishes*. New York: Springer-Verlag, pp. 395–426.
- Norris KS, Dohl T (1980) Structure and function of cetacean schools. In: Herman LM (ed) *Cetacean Behavior: Mechanisms and Functions*. New York: John Wiley & Sons, pp. 230–244.
- Norris KS, Evans EC (1988) On the evolution of acoustic communication systems in vertebrates. Part II: Cognitive aspects. In: Nachtigall PE, Moore PWB (eds) *Animal Sonar: Processes and Performance*. New York: Plenum Press, pp. 671–682.
- Norris KS, Møhl B (1981) Can odontocetes stun prey with sound? *Am Nat* 122:85–104.
- Norris KS, Prescott JH, Asa-Dorian PV, Perkins P (1961) An experimental demonstration of echolocation behavior in the porpoise, *Tursiops truncatus*, Montagu. *Biol Bull* 120:163–176.
- Norris KS, Würsig B, Wells RS, Würsig M (1994) *The Hawaiian Spinner Dolphin*. Berkeley: University of California Press.
- Oehen S (1996) The acoustic behavior of the bottlenose dolphins *Tursiops truncatus* in the Northern Adriatic Sea. Masters Thesis, Zoo Museum, University Zurich, Zurich, Switzerland.
- Ostman J (1994) Social organization and social behavior of Hawaiian spinner dolphins (*Stenella longirostris*). Ph.D. Dissertation. University of California, Santa Cruz, CA.
- Overstrom NA (1983) Association between burst-pulse sounds and aggressive behavior in captive Atlantic bottlenose dolphins (*Tursiops truncatus*). *Zool Biol* 2:93–103.
- Pack AA, Herman LM (1995) Sensory integration in the bottlenose dolphin: immediate recognition of complex shapes across the sense of echolocation and vision. *J Acoust Soc Am* 98:722–733.
- Payne R, Webb D (1971) Orientation by means of long range acoustic signaling in baleen whales. *Ann NY Acad Sci* 188:110–141.
- Popper AN, Hawkins HL, Gisiner RC (1997) Questions in cetacean bioacoustics: some suggestions for future research. *Bioacoustics* 8:163–182.
- Pryor K (1986) Reinforcement training as interspecies communication. In: Schusterman RJ, Thomas JA, Wood FG (eds) *Dolphin Cognition and Behavior: A Comparative Approach*. Hillsdale, NJ: Lawrence Erlbaum Associates, pp. 253–260.
- Pryor K, Kang I (1980) Social behavior and school structure in pelagic porpoises (*Stenella attenuata* and *S. longirostris*) during purse seining for tuna. La Jolla, CA: Natl Mari Fish Serv, SW Fisheries Center. Adm Report LJ-80-11c, p. 86.

- 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: Pryor K, Norris KS (eds) *Dolphin Societies: Discoveries and Puzzles*. Berkeley: University of California Press, pp. 161–196.
- Raloff J (1996) In noise a neural necessity? *Sci News* 150:330–331.
- Ralston JV, Herman LM (1989) Dolphin auditory perception. In: Dooling JR, Hulse SH (eds) *Complex Acoustic Perception: The Comparative Psychology of Complex Acoustic Perception*. Hillsdale, NJ: Lawrence Erlbaum Associates, pp. 295–338.
- Reiss D (1988) Observations on the development of echolocation in young bottlenose dolphins. In: Nachtigall PE, Moore PWB (eds) *Animal Sonar Systems*. Helsingør, Denmark: Plenum Press, pp. 121–127.
- Richards DG, Wolz JP, Herman LM (1984) Vocal mimicry of computer-generated sounds and vocal labeling of objects by a bottlenosed dolphin, *Tursiops truncatus*. *J Comp Psychol* 94:1–10.
- Richardson WJ, Greene CR, Malme CI, Thomson DH (1995) *Marine Mammals and Noise*. San Diego: Academic Press.
- Rigley L (1983) Dolphins feeding in a South Carolina salt marsh. *Whalewatcher* 17:3–5.
- Roitblat HL, Au WWL, Nachtigall PE, Shizumura R, Moons G (1995) Sonar recognition of targets embedded in sediment. *Neur Networks* 8:1263–1273.
- Rossbach KA, Herzing DL (1997) Underwater observations of benthic-feeding bottlenose dolphins (*Tursiops truncatus*) near Grand Bahama Island, Bahamas. *Mar Mamm Sci* 13:498–504.
- Savage-Rumbaugh ES (1994) *Kanzi*. New York: John Wiley & Sons.
- Savage-Rumbaugh ES, McDonald K, Sevcik R, Hopkins W, Rupert E (1986) Spontaneous symbol acquisition and communicative use by pygmy chimpanzees (*Pan paniscus*). *J Exp Psychol* 115:111–135.
- Sayigh LS, Tyack PL, Wells RS, Scott MD (1990) Signature whistles of free-ranging bottlenose dolphins *Tursiops truncatus*: stability and mother-offspring comparisons. *Behav Ecol Sociobiol* 26:247–260.
- Schultz KW, Corkeron PJ (1994) Interspecific differences in whistles produced by inshore dolphins in Moreton Bay, Queensland, Australia. *Can J Zool* 72:1061–1068.
- Schultz KW, Cato DH, Corkeron PJ, Bryden MM (1995) Low frequency narrow-band sounds produced by bottlenose dolphins. *Mar Mamm Sci* 11:503–509.
- Schusterman RJ (1990) Stimulus equivalence and cross-modal perception: a testable model for demonstrating symbolic representations in bottlenose dolphins. In: Thomas JA, Kastelein RA (eds) *Sensory Abilities of Cetaceans*. New York: Plenum Press, pp. 677–684.
- Seyfarth RM, Cheney DL (1980) The ontogeny of vervet monkey alarm-calling behavior: a preliminary report. *Z Tierpsych* 54:37–56.
- Seyfarth RM, Cheney DL, Marler P (1980) Vervet monkey alarm calls: semantic communication in a free-ranging primate. *Anim Behav* 28:1070–1094.
- Shane SH (1990) Behavior and ecology of the bottlenose dolphin at Sanibel Island, Florida. In: Leatherwood S, Reeves RR (eds) *The Bottlenose Dolphin*. San Diego: Academic Press, pp. 245–266.
- Shennan GC, Waas JR, Lavery RJ (1994) The warning signals of parental convict cichlids are socially facilitated. *Anim Behav* 47:974–976.

- Simila T, Ugarte F (1993) Surface and underwater observations of cooperatively feeding killer whales in northern Norway. *Can J Zool* 71:1494-1499.
- Simmons JA, Saillant PA, Ferragamo MJ, Haresign T, Dear SP, Fritz J, McMullen TA (1996) Auditory computations for biosonar target imaging in bats. In: Hawkins HL, McMullen TA, Popper AN, Fay RR (eds) *Auditory Computation*. New York: Springer-Verlag, pp. 401-460.
- Simmons JQ, Baltaxe C (1975) Language patterns of adolescent autistics. *J Autism Childh Schizo* 5:333.
- Sjare BL, Smith TG (1986) The vocal repertoire of white whales, *Delphinapterus leucas*, summering in Cunningham Inlet, Northwest territories. *Can J Zool* 64:407-415.
- Slooten E (1994) Behavior of Hector's dolphin: classifying behavior by sequence analysis. *J Mamm* 75:956-964.
- Smith WJ (1977) *Behavior of Communicating*. Cambridge: Harvard University Press.
- Smolker RA, Mann J, Smuts BB (1993) Use of signature whistles during separations and reunions by wild bottlenose dolphin mothers and infants. *Behav Ecol Sociol* 33:393-402.
- Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT (1987) *Primate Societies*. Chicago: University of Chicago Press.
- Struhsaker TT (1967) Auditory communication among vervet monkeys (*Cercopithecus aethiops*). In: Altman SA (ed) *Social Communication Among Primates*. Chicago: University of Chicago Press, pp. 281-324.
- Taruski AG (1979) The whistle repertoire of the North Atlantic pilot whale (*Globicephala melaena*) and its relationship to behavior and environment. In: Winn HE, Olla BL (eds) *Behavior of Marine Animals: Current Perspectives in Research*. New York: Plenum Press, pp. 345-368.
- Tavolga WN (1983) Theoretical principles for the study of communication in cetaceans. *Mammalia* 47:3-26.
- Tavolga MC, Essapian FS (1957) The behavior of the bottlenose dolphin, *Tursiops truncatus*: mating, pregnancy and parturition, mother-infant behavior. *Zoologica* 42:11-31.
- Thomsen F (1995) Whistles as close range emotive signals in wild killer whales (*Orcinus orca*) off Vancouver island, British Columbia, Canada. Masters Thesis. University of Hamburg, Hamburg, Germany.
- Turl CW (1993) Low-frequency sound detection by a bottlenose dolphin. *J Acoust Soc Am* 94:3006-3008.
- Tyack P (1993) Animal language research needs a broader comparative and evolutionary framework. In: Roitblat HL, Herman LM, Nachtigall PE (eds) *Language and Communication—Comparative Perspectives*. Hillsdale, NJ: Lawrence Erlbaum Associates, pp. 1115-1138.
- van Hooff JARAM (1982) Categories and sequences of behavior: methods of description and analysis. In: Scherer KR, Ekman P (eds) *Handbook of Methods in Nonverbal Behavior Research*. New York: Cambridge University Press, pp. 362-439.
- Vel'min VA, Dubrovskii NA (1978) Auditory perception by bottlenose dolphins of pulsed sounds. In: Sokolov VYE (ed) *Marine Mammals: Results and Methods of Study*. Moscow: Nauka Publications, pp. 90-98.
- von der Emde G (1988) Greater horseshoe bats learn to discriminate simulated echoes of insects fluttering with different wingbeat rates. In: Nachtigall PE, Moore

- PWB (eds) *Animal Sonar: Processes and Performance*. New York: Plenum Press, pp. 495-499.
- Wang D, Würsig B, Evans W (1995) Comparisons of whistles among seven odontocete species. In: Kastelein RA, Thomas JA, Nachtigall PE (eds) *Sensory Systems of Aquatic Mammals*. Woerden, Netherlands: De Spil, pp. 299-324.
- Watkins WA (1967) The harmonic interval: fact or artifact in spectral analysis of pulse trains. In: Tavolga WN (ed) *Marine Bioacoustics*, Vol 2. New York: Pergamon Press, pp. 15-43.
- Watkins WA, Schevill WE (1974) Listening to Hawaiian spinner porpoise, *Stenella cf. longirostris*, with a three-dimensional hydrophone array. *J Mamm* 55:319-328.
- Watkins WA, Schevill WE (1977) Sperm whale codas. *J Acoust Soc Am* 62:1485-1490.
- Wells RS, Scott MD, Irvine AB (1987) The social structure of free-ranging bottlenose dolphins. In: Genoways HH (ed) *Current Mammalogy*, Vol 1. New York and London: Plenum Press, pp. 247-305.
- Wood FG 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 FG, Caldwell DK, Caldwell MC (1970) Behavioral interactions between porpoises and sharks. In: Pilleri G (ed) *Investigations on Cetacea*, Vol 2. Berne, Switzerland: University of Berne, Brain Anatomy Institute, pp. 264-277.
- Würsig B, Kieckhefer TR, Jefferson TA (1990) Visual displays for communication in cetaceans. In: Thomas JA, Kastelein RA (eds) *Sensory Abilities of Cetaceans*. New York: Plenum Press, pp. 545-559.
- Xitco MJ (1988) Mimicry of modeled behaviors by bottlenose dolphins. Masters Thesis. University of Hawaii, Honolulu, HI.
- Xitco MJ (1996) Referential pointing by bottlenose dolphins. Ph.D. Dissertation. Southern Methodist University, Houston, TX.
- Xitco MJ, Roitblat HL (1996) Object recognition through eavesdropping: passive echolocation in bottlenose dolphins. *Anim Learn Behav* 24:355-365.