

## Social and Nonsocial Uses of Echolocation in Free-Ranging *Stenella frontalis* and *Tursiops truncatus*

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### Introduction

Dolphins have sophisticated acoustic processing, echolocation abilities, and anatomical structures (Au 1993; Cranford, Amundin, and Norris 1996; Ketten 1997). Measuring parameters of echolocation signals primarily has occurred with physically restricted dolphins (Au 1993). Only recently have real-time recordings of echolocation signals been acquired in the wild (Au, Herzing, and Aubauer 1998). Although many aspects of sound use by dolphins have been reported (Herman and Tavolga 1980; Au 1993), most are in captivity or in field sites where behavior is often inferred through surface activity. Although interesting, the interpretation of surface behavior lacks sufficient visual confirmation to determine what the animals are actually doing under the water while signals are being recorded. It is more likely that correlating visually observable and verifiable behaviors with sound use will be an unbiased and productive approach without the problems inherent with observer inference of underwater behavior from the presence, or lack of, surface behavior. Unfortunately, there are only a few study sites in the world where dolphins can be observed on a regular basis engaging in a variety of normal behaviors. Specific behavioral and spectral descriptions of bottlenose dolphins (*Tursiops truncatus*, *T.t.*) foraging in the sand (Herzing 1996; Rossbach and Herzing 1997) and Atlantic spotted dolphins (*Stenella frontalis*, *S.f.*) using echolocation during foraging and social behavior (Herzing 1996) have been reported. Since behavioral definitions of underwater observations are less subjective than surface observations, substantiated visual observation should be required in the interpretation of the function of echolocation and other signals. This chapter offers a further detailed description of underwater visual and acoustic observations made during social and nonsocial behavior of free-ranging Atlantic spotted and bottlenose dolphins in the Bahamas from 1989 to 1998. Echolocation observations are placed in (1) behavioral contexts, by specific activity categories, and (2) ecological contexts, by describing specific habitats, depth of water, prey items, and bottom substrate. It is hoped that by reporting the use of echolocation signals during a variety of underwater behavioral contexts and specific eco-

logical habitats, the functional use of these signals can be explored fully. Improved methods of capturing these signals, in a full-bandwidth capacity and in a real-life and observable field site, will be explored in the future.

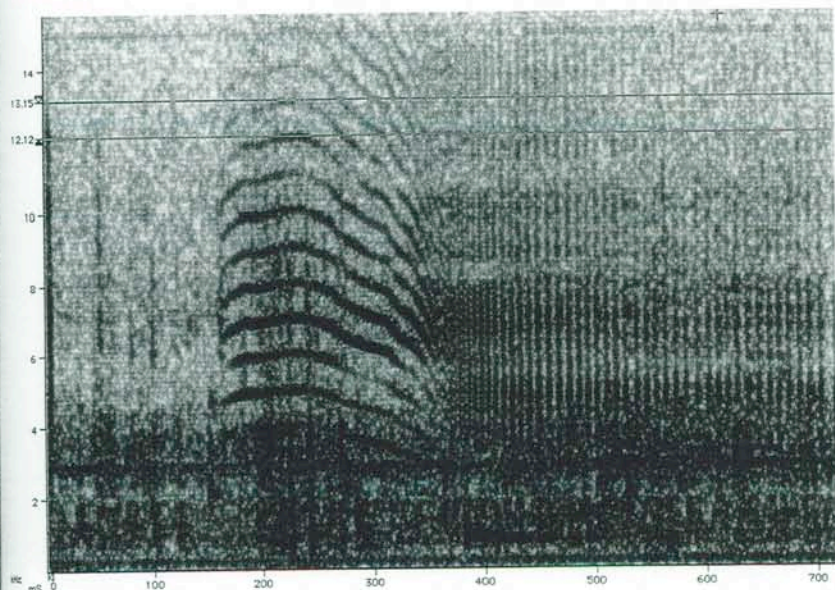
### Materials and Methods

The Bahama Islands are an archipelago in the tropical West Atlantic east of Florida. Although surrounded by deep water and the Florida straits, the water here is shallow (<15 m). The Bahamian banks are thick, submerged platforms of calcareous rock providing diverse habitats, including fringe and patch reefs, atolls, grassy flats, and ledges.

Since 1985, a resident community of approximately 220 spotted and 200 bottlenose dolphins have been identified, sexed, and observed in a variety of behavioral contexts in this region (Herzing 1996, 1997). During each underwater observation data were collected on group size, habitat type, environmental conditions, individual identity, age class, and behavioral context. Underwater behavioral and sound data were recorded for each encounter using underwater video cameras (Sony TR700, Yashica KV1, Sony Digital TR200) with a Labcore 76 hydrophone with frequency to 20 kHz and sensitivity of  $-192$  dB re  $1 \mu\text{Pa}$  input to assure simultaneous recordings of underwater behavior and sounds. Ad libitum and behavioral event sampling was used to record foraging and social activity.

Individual click trains, or social sounds, were chosen for analysis when dolphins were alone and echolocating on bottom, playing with objects, or physically orienting/approaching another dolphin. The full-bandwidth recording of echolocation signals was not possible because (1) such mobile/remote equipment did not exist for underwater use, and (2) in the wild, the angle at which the dolphins orient during natural behavior cannot be controlled (resulting in the inability to assure the collection of head-on high-frequency signals). Unlike surface studies, where the underwater activity of echolocating dolphins is often inferred (based on the presence or absence of surface behaviors), the strength of these underwater observations include (1) our ability to observe visually underwater, and on a regular and repeated basis, the





**Fig. 56.1.** Spectrogram of a high-repetition-rate, burst-pulsed sound grading to a click train with a slow repetition rate. High repetition rates are more easily measured by harmonic artifact intervals (vertical cursors) than individual clicks (horizontal cursors) as described by Watkins (1967).

actual activities of dolphins during echolocation, and (2) the recording click rates that can be extracted with narrowband recordings and when dolphins are recorded from a side angle. The recording and analysis of click rates (in lower frequencies and off-axis) are not restricted to full-bandwidth recording equipment and are a viable parameter to measure during echolocation.

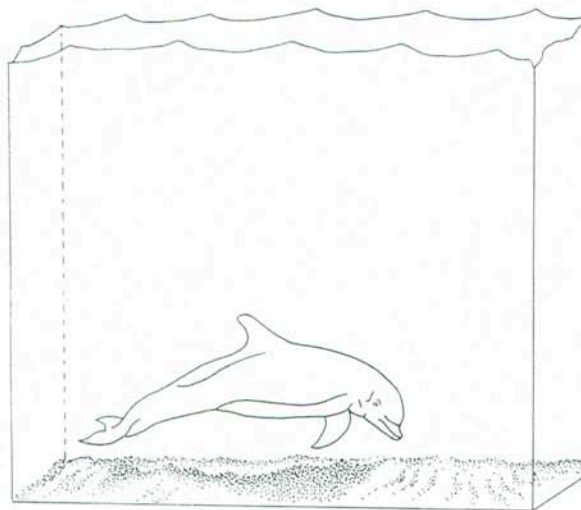
Click repetition rates were extracted using Spectral Innovations MacDSP hardware and software. Click rates were individually counted, or, when repetition rates were high, the harmonic artifact feature representing repetition rate (as described in Watkins 1967) was used (fig. 56.1).

## Results

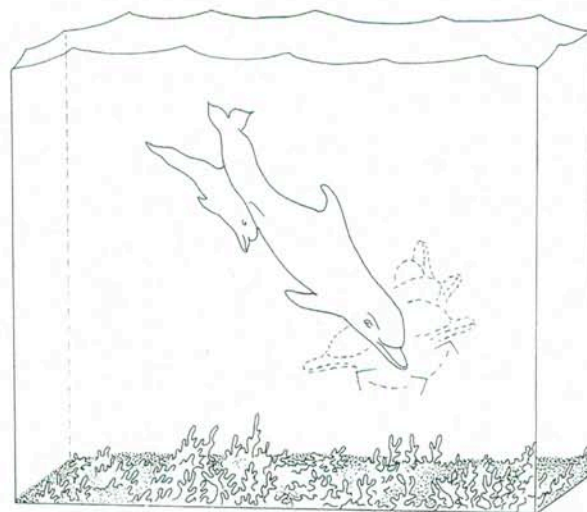
### NONSOCIAL USES OF ECHOLOCATION: SEARCH AND APPROACH STRATEGIES

From 1989 to 1998, 306 observations of foraging and 751 of social behavior were made. The average duration of an observation was 20 min. The 159 spotted (*S.f.*) and 147 bottlenose (*T.t.*) dolphin foraging observations can be categorized as follows: horizontal and vertical scanning (32, *S.f.*; 103, *T.t.*), surface chases (83, *S.f.*; 25 *T.t.*), ledge/hole feeding (0, *S.f.*; 6, *T.t.*), percussive jaw-claps/tail-hits (4, *S.f.*; 5, *T.t.*), and rostrum hits (40, *S.f.*; 8, *T.t.*).

Table 56.1 displays the types of foraging strategies observed along with habitat information, prey types, and postural/vocal behavior. Concomitant visual behaviors are depicted in figs. 56.2–56.8. The strategy of searching was substrate and prey specific. Two phases of echolocation during foraging were observed, the search phase and the approach phase. In the search phase, dolphins actively searched using body or head movement. During this phase dolphins were either stationed in the water column (up to 15 m) scanning down, or near the bottom scanning <1 m off the sand. Echolocation click rates were



**Fig. 56.2.** Horizontal bottom scanning occurs while the dolphin moves along sandy bottom.



**Fig. 56.3.** Vertical water-column scanning occurs while the dolphin hovers in a stationary position above the bottom.



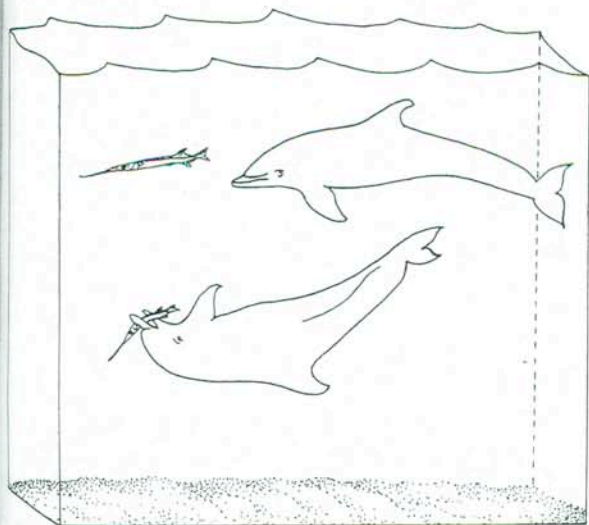
**TABLE 56.1.** Foraging strategies by Atlantic spotted dolphin (*Stenella frontalis*: S.f.) and bottlenose dolphin (*Tursiops truncatus*: T.t.). Species key: (A) conger eels (family Congridae); (B) snake eels (family Ophichthidae); (C) razorfish/wrasses (family Labridae); (D) flying fish (family Exocoetidae); (E) needlefish (family Belonidae); (F) ballyhoo (family Hemiramphidae); (G) flounder (family Bothidae); (H) snakefish (family Synodontidae); (I) grunts (family Pomadasyidae); (J) squirrelfish (family Holocentridae).

Strategy	Habitat	Foraging depth	Prey	Postural behavior	Echolocation observations
Horizontal bottom scanning (T.t., S.f.)	Dense or loose sand, no grass	<.5 m from bottom	Deeply buried fish (A, B, C)	Head bent to right and angled downward. Upon detection dolphin tips body and "digs" with rostrum.	Click rates 200 Hz, increasing to 500 Hz when digging in sand (Herzog 1996)
Vertical water-column scanning (T.t., S.f.)	Turtle grass beds, algae covered sand	3–15 m from bottom	Deeply buried fish (A, B, C)	Dolphin stationary, head bent to right, angled downward. Head rotation clockwise-counterclockwise.	Click rates 20–200 Hz when audible. Calf may be positioned under adult and mimic movements of head.
Surface scanning (T.t., S.f.)	Water surface, air surface	At surface	Schooling or moving fish (D, E, F)	Dolphin swims upright scanning; may turn inverted during chase, catch	Rapid echolocation clicks with increasing repetition rate with proximity to target
Ledge, hole scanning (T.t., only)	Coral reef, rocky bottom	<.5 m from substrate	Hidden fish (I, J)	Rostrum directed under ledges or in holes. Dolphin grabs fish under ledge or hole.	Click rates 8–100 Hz, with whistles and trills
Percussive jaw claps (T.t., S.f.)	Scattered benthic sargassum	<.5 m from bottom	Deeply buried fish (A, B, C)	Head bent downward during intermittent jaw claps. Dolphin moves along bottom slowly	May or may not echolocate during behavior
Percussive rostrum bop (T.t., S.f.)	Dense or loose sand	On bottom or <.5 m	Shallow buried fish (G, H)	Dolphin stops during bottom scanning and strikes bottom multiple times with tip of rostrum until fish darts out and chase ensues.	Scanning clicks audible during bottom scanning and increased repetition rates during rostrum hits.
Percussive tail slaps and pectoral fin hits (T.t., S.f.)	Dense or loose sand	<.5 m from bottom	Deeply buried fish (A, B, C)	Dolphin moves along bottom, striking sand with appendage and dolphin returns to vortex for fish.	May have associated echolocation clicks during horizontal scanning on bottom and retrieval of fish.

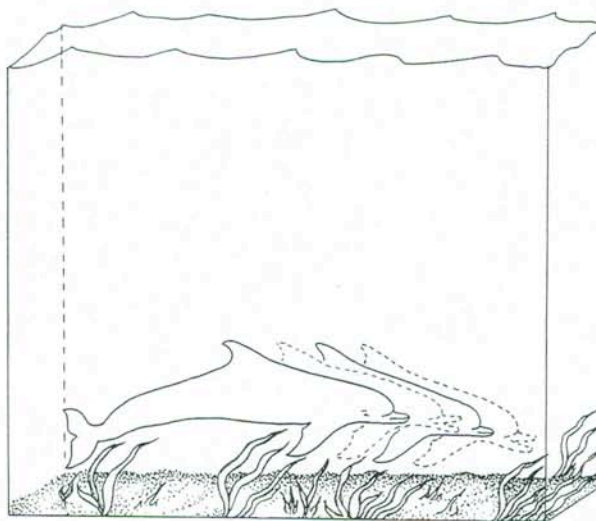
slow (<200 Hz) until the approach phase, when, after detection, dolphins emitted increasing repetition rates of clicks (up to 500 Hz) while pointing into the sand and digging out prey. Other techniques, such as percussive sounds or the physical disturbance of the sand, were used before the approach phase and appeared to create supplemental information and access to prey.

Various surveillance strategies were observed for *Stenella* during rest and travel (table 56.2). These include underwater observation of echolocation activity and be-

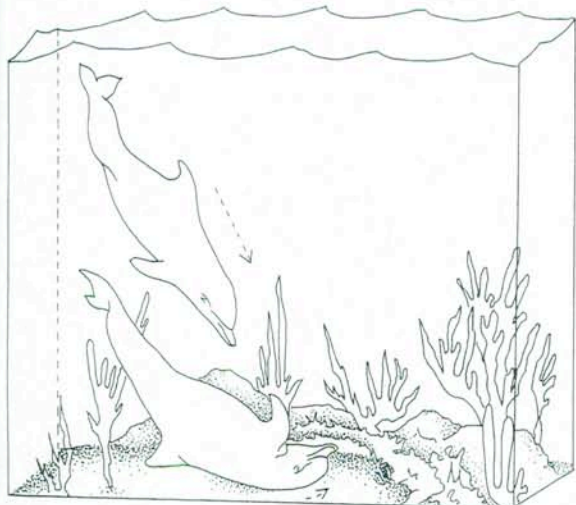
havior such as age-class specific reactions to predators such as sharks. The primary mode of monitoring was listening in both clear and murky waters. During twilight hours and in deep water (>30 m), dolphins were observed underwater and did not employ active, audible (<15 kHz) echolocation until an apparent cue was detected and warranted inspection. Postdetection behavior included slow-rate echolocation clicks (8–20 Hz), close, physical contact within the dolphin group, and coordinated head scanning toward the bottom.



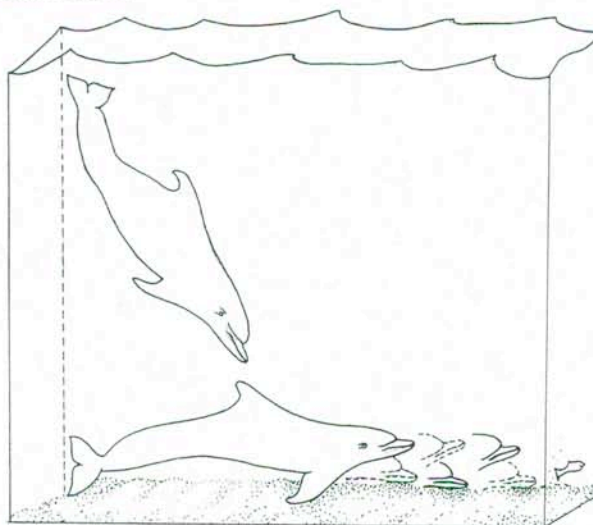
**Fig. 56.4.** Water surface/air interface scanning occurs as the dolphin works underneath the surface of the water.



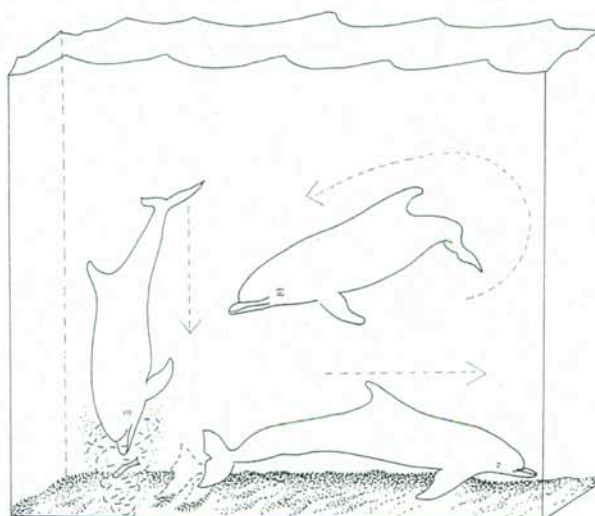
**Fig. 56.6.** Percussive jaw-claps occur as the dolphin is moving along bottom.



**Fig. 56.5.** Ledge/hole scanning occurs as the dolphin searches and explores under substrate.



**Fig. 56.7.** Percussive rostrum hits occur as the dolphin is on bottom. Rostrum makes shallow and intermittent contact into sand.

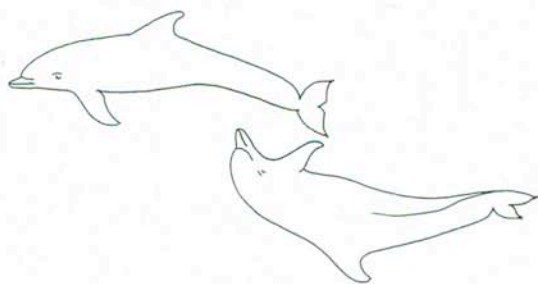


**Fig. 56.8.** Percussive tail-slaps and pectoral fin hits occur as the dolphin moves along bottom. The dolphin may turn and seek out the vortex of sand and then dig in the center for fish.



TABLE 56.2. Surveillance strategies of Atlantic spotted dolphins (*Stenella frontalis*).

Behavioral observation	Echolocation observation	Age/class	Reaction
Daytime rest and travel	Quiet and passive vigilance	All	None
Acoustic cue of predator	Slow echolocation 8–20 Hz	All	Head-scanning and tightening of group
Predator in visual range			
• Tiger/bull sharks	Echolocation may stop while predator in sight	Mothers and calves	Sink to bottom and flee as group
• Tiger sharks	Social signals: excitement vocalization or signature whistles	Calves	Panic and erratic swimming
• Hammerheads and nurse sharks	Active echolocation and buzzing of predator	Mixed age/classes	Vigilance or active chasing of predator
• Bull sharks	Quiet	Old adults	Sink to bottom and remain motionless



**Fig. 56.9.** Genital inspection and buzzing is typical during courtship and disciplinary behavior.

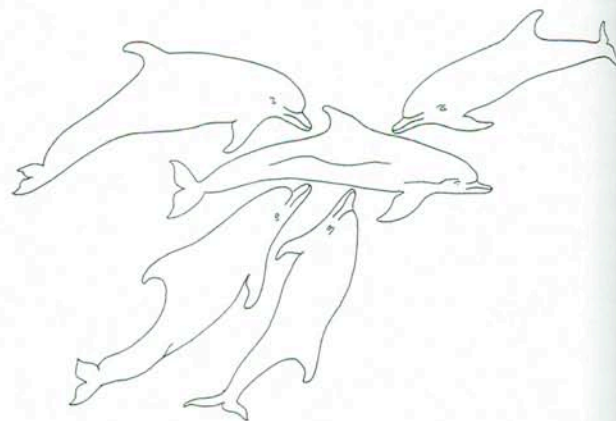
#### SOCIAL USES OF ECHOLOCATION: CONSPECIFIC BUZZING AND SCANNING

The use of high-repetition-rate click trains during social interaction (genital buzzes of 8–2000 Hz, squawks of 200–1200 Hz—as described in Herzing 1996) were observed during social behavior including courtship (fig. 56.9), discipline and play (fig. 56.10), aggression (fig. 56.11), and during focused attention to inanimate objects (fig. 56.12). Clicks within such close proximity and with high repetition rates are not believed to have an echolocation function according to current sonar theory. To determine the possibility of tactile components to these sounds, Kolchin and Bel'kovich's (1973) pressure amplitude measurement threshold levels (10–40 mg/mm<sup>2</sup>) for tactile sensitivity in the common dolphin (*Delphinus delphis*) were converted to sound pressure levels (SPL in dB re 1  $\mu$ Pa), where

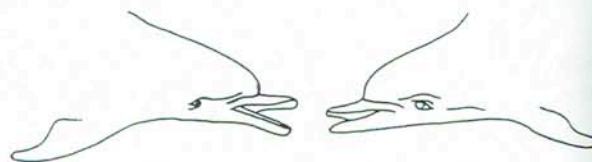
$$\begin{aligned}
 1 \mu\text{Pa} &= 10^{-6} \text{ kg/ms}^2 \\
 \text{gravity (g)} &= 9.8 \text{ m/s}^2 \\
 \text{mg/mm}^2 &= 10^{-6} \text{ kg}/10^{-6} \text{ m}^2 = \text{kg/m}^2
 \end{aligned}$$

then

$$\begin{aligned}
 P1 &= 10 \text{ mg/mm}^2 \times g = 10 \text{ kg/m}^2 \times 9.8 \text{ m/s}^2 = 98 \\
 Pa &= 98 \times 10^6 \mu\text{Pa} \text{ and } \text{SPL} = 20 \log P1 = 160 \text{ dB re } 1 \mu\text{Pa} \\
 P2 &= 40 \text{ mg/mm}^2 \times g = 40 \text{ kg/m}^2 \times 9.8 \text{ m/s}^2 = 392 \\
 Pa &= 392 \times 10^6 \mu\text{Pa} \text{ and } \text{SPL} = 20 \log P2 = 172 \text{ dB re } 1 \mu\text{Pa}
 \end{aligned}$$



**Fig. 56.10.** Group buzzing occurs when one dolphin floats passively while others buzz it, usually in the midbody area.



**Fig. 56.11.** Head-to-head orientation and buzzing occur during aggressive behavior and juvenile play. Dolphins may be moving or stationary.



**Fig. 56.12.** Exploratory object buzzing is typical on objects, including floating debris and plant life.

Therefore, it would take SPL levels of 160–172 dB re 1  $\mu$ Pa to stimulate the dolphin's somatic pressure receptors. Peak source levels as high as 210 dB re 1  $\mu$ Pa were recently measured for these resident *Stenella frontalis* (Au, Herzing, and Aubauer 1998), which are above the



amplitude levels required to pass the estimated levels for somatic sensation.

## Discussion

### NONSOCIAL USES OF ECHOLOCATION

Atlantic spotted dolphins (*Stenella frontalis*) and bottlenose dolphins (*Tursiops truncatus*) in our study used echolocation for both social and nonsocial uses. Scanning strategies during foraging included (1) horizontal bottom scanning, (2) vertical water-column scanning, (3) surface scanning, and (4) ledge/hole scanning. The presence of specific substrate or algae, depth of water, and the prey species determined the scanning techniques. Deeply buried prey were retrieved using a variety of techniques including percussive elements such as jaw-claps, tail-slaps, and pectoral fin strikes. Shallow-buried species were retrieved with direct horizontal scanning or the use of physical blows of the rostrum on the bottom to encourage the fish to move and presumably be detected moving along the sandy bottom. Dolphins scanned vertically, and from great distances, in areas of dense grass or other bottom clutter. Detection seemed to occur from these distances and did not require more horizontal scanning on the bottom. Instead, the dolphins went directly down to the bottom from the midwater column and dug out a fish. For schooling fish, dolphins arched their bodies during the chase to presumably accommodate the projection of clicks. Just before capture, dolphins often turned upside down, possibly utilizing their visual system at this stage of capture. The variety of strategies mirrored the variety of habitats and prey species, suggesting that dolphins use a multitude of behavioral and acoustic strategies in sophisticated anticipation of their prey's behavior and the effects of their sound in cluttered/uncluttered environments. Although different than bat echolocation (Au 1997), dolphin echolocation is used in habitat exploration (cluttered versus uncluttered) and for monitoring escape strategies of prey (move, dig, freeze). Both suggest that dolphins recognize specific prey and employ species-specific strategies.

Dolphins also employed various monitoring and vigilance strategies and were typically silent listeners unless cues were received that triggered active inspection. To what degree do dolphins use passive listening versus active echolocation in other locations? Barros and Wells (1998) reported that bottlenose dolphins target soniferous prey, suggesting that passive listening is employed in detection.

Clicks and pulsed sounds have similar acoustic features, with the primary difference being time intervals between pulses. A slight change in this interval can make a large difference in aural perception to both the human ear and to the visual representation on a spectrogram. The fact that click trains grade into pulsed sounds with gradual decreases in interclick intervals, and often without a change in peak frequency (Murray 1997; Herzing

1988), should caution us against making discrete functions out of purely aural differences. Although the two-way transit time interval rule (needed to explain currently understood echolocation functions of clicks) no longer holds during click trains that grade into high-repetition-rate pulsed sounds, the animals are clearly using them in a continuum of motion and activity. Perhaps it is our definition of the functions of such clicks that needs to be expanded, rather than separating the explanation based on our understanding of how biological sonar may work. The measuring of echolocation signals by moving dolphins, rather than stationary subjects, is already illuminating challenges to current sonar theories (Sigurdson 1998).

### SOCIAL USES OF ECHOLOCATION

The social uses of click trains reported here included low-frequency buzzing during courtship, discipline, play, aggression, and exploration. Source levels adequate for tactile stimulation have been measured in spotted dolphins (Au, Herzing, and Aubauer 1998) and for multiple delphinid species (Au 1993). Ketten (1997) described the frequency-specific sound-conduction properties of various parts of the dolphin's rostrum. This suggests that jaw rotation, open-mouth behavior, and head rotation could be comparable to sound focusing and ear rotation in bats. Intense, close proximity sounds and percussive elements, that theoretically provide tactile sensation, have been recorded in intraspecific aggression (Overstrom 1983; Herzing 1996), interspecific aggression (Herzing and Johnson 1997), and possibly fish stunning (Norris and Møhl 1981; Marten et al. 1988; Marten et al. 2001). The use of high-repetition click trains suggests that odontocetes use "shorter than transit time" intervals, and packets of clicks (burst-pulsed sounds) could also be manipulated in an "echolocation type" way to provide both social and prey information. The proximity and angle of calves underneath scanning mothers (fig. 56.3), parameters critical for eavesdropping (Xitco and Roitblat 1996), support the idea that learning opportunities are available during foraging behavior in the wild. In the Bahamas, observations of young calves echolocating on small flounders, and following conspecifics during foraging, suggest that echolocation skills may begin very early in life. Spotted dolphins nurse as long as five years but are weaned gradually and learn to catch fish in the first year of life (Herzing 1997). The development of echolocation abilities and its directed use may be critical for survival in the wild. In captivity, the use of echolocation signals by bottlenose dolphin calves has been reported as early as six months (Reiss 1988).

## Conclusion

The use of high-repetition-rate click trains (higher than defined by current sonar theory to be of echolocation value), during both social and nonsocial activity, may



indicate uses of echolocation clicks not previously recorded. High rates of clicks have been reported by Watkins (1967) in the harbor porpoise (*Phocoena phocoena*) at 700 Hz, Risso's dolphin (*Grampus griseus*) at 250–330 Hz, in bottlenose and Atlantic spotted dolphins at 2000 Hz (Herzing 1988, 1996). Murray (1997) reported click trains grading into pulsed sounds with decreasing interclick intervals (<2 ms). Gradation of click trains, to pulsed sounds to whistles, without a change in peak frequency, has been described elsewhere (Herzing 1988; Watkins 1967) and is strong evidence that decreasing interclick intervals during click trains are a graded and continuous event. Whether the function of such clicks is also continuous, as far as informational content, is not clear.

Why would dolphins use click rates so high that individual pulses are no longer distinguishable and separated by adequate transit times to discriminate one outgoing click from another? Whether such high rates of clicks are useful for return echolocation information (i.e., signals with transit times long enough to allow the return echo to be received before the next one is sent out) or have a tactile effect on a target, in their ability to escape, is unknown. The fact that dolphins play and buzz animate and inanimate objects, when echolocation information about an already visual and captive target are not needed, may suggest that there is another function

for high-repetition click trains other than echolocation. Evans and Powell (1967) reported repetition rates of 200 Hz from dolphins 0.5 m from a target. Relative geometry of the dolphin's head to the sand, such as a more vertical angle, and rotation of that angle (e.g., through rostrum movement up and down, or upside-down inverting swimming), would also change the angle of the echolocation beam to the target. Our abilities to measure such subtle aspects of echolocation signals, with moving dolphins, would greatly increase our understanding of the use of echolocation during natural behavior. The development of a self-contained, mobile underwater video and full-bandwidth recording unit would ensure complete sound and visual signal collection during the activity of dolphins, thus removing the potential misinterpretation of signals recorded during surface-only studies.

### Acknowledgments

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## { 57 }

### Variable Spectra and Nondirectional Characteristics of Clicks from Near-Surface Sperm Whales (*Physeter catodon*)

William A. Watkins and Mary Ann Daher

#### Introduction

The first positive attribution of click sounds to sperm whales (*Physeter catodon*) was by Worthington and Schevill in 1957; detailed study of the acoustic behavior of these whales began in 1958 (Schevill and Watkins 1962). Results from these and subsequent studies included the following assessments of their use of sound: whales often clicked at regular rates during dives for minutes at a time, interspersed with silences of variable duration; no clicks were heard from lone whales; those near the surface produced few clicks; short click series,

called codas (Watkins and Schevill 1977b), appeared to have a communicative function; young (7–8 m) whales were responsible for most aerial displays and often produced long click sequences with highly variable click rates. Clicks from near-surface whales recorded during more than 100 cruises (Woods Hole Oceanographic Institution, WHOI) consistently had variable spectra and no apparent propagation directionality. These sperm whale clicks appeared to be used mostly for communication (Watkins 1977).

Sperm whales produce broadband click sounds with frequencies from about 100 Hz to 30 kHz. They click