CETACEAN BEHAVIOR
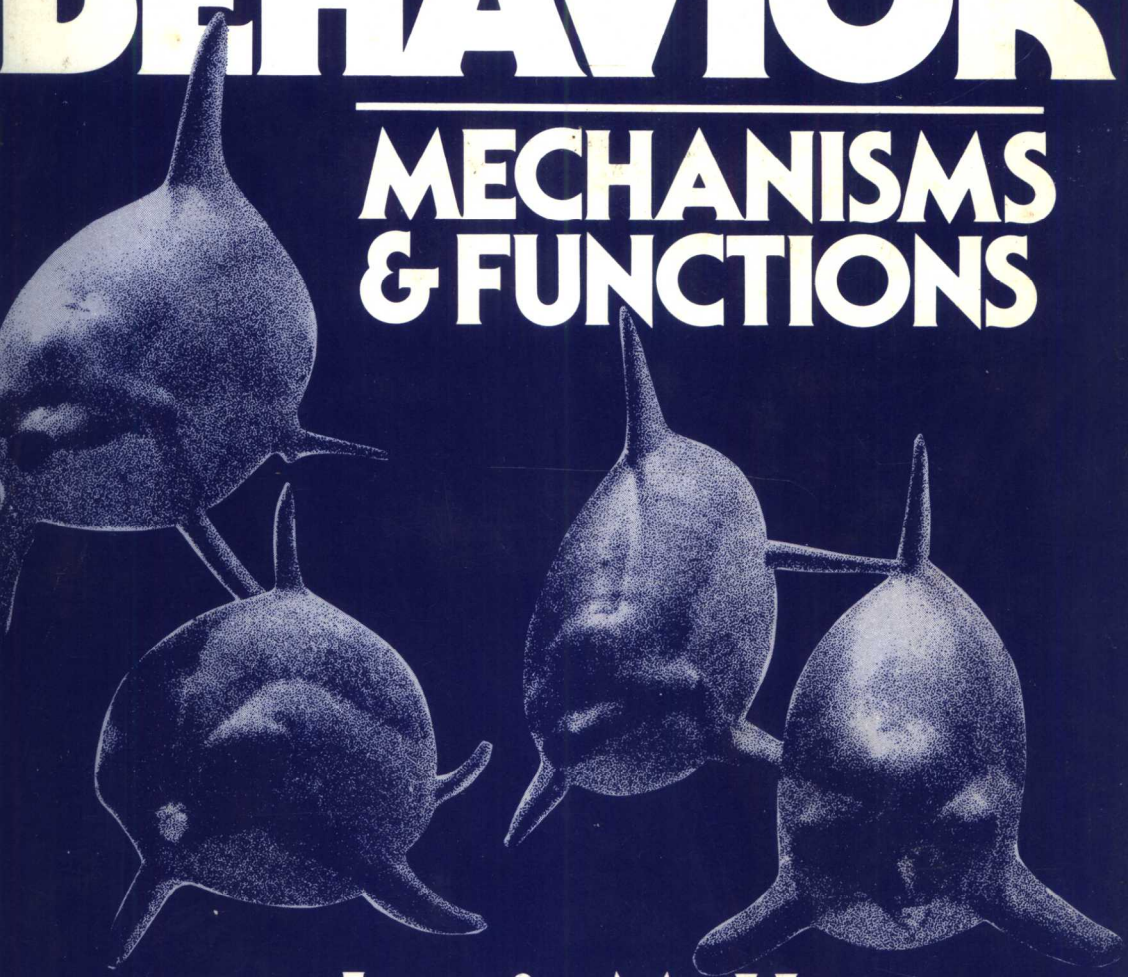
MECHANISMS & FUNCTIONS

Edited by Louis M. Herman

Cetacean Behavior:

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Preface

As an outgrowth of the heightened concern for the protection and conservation of marine mammals, the decade of the 1970s witnessed greatly increased efforts in the study of whales, dolphins, and porpoises. In organizing this volume, the goal was to provide a broad, tutorial review of current data and theory on selected aspects of cetacean behavior, combined, where possible, with new information generated by the authors. It was hoped that the collection of reviews would provide a source of background material and some new insights for workers in the field and for students interested in the study of the cetaceans.

Behavior is influenced and shaped by the perceived world, and hence a description of the major sensory mechanisms for extracting information from the world is given. Audition, a sense that appears to be primary in the life of all cetaceans is reviewed by Popper; and vision, a sense that may be more important than normally suspected, is reviewed by Dawson. Comments are given on both the structural and functional aspects of these sensory systems. Briefer discussions of the tactile and gustatory senses are contained within portions of the chapter on communication by Herman and Tavolga.

Behavior takes place within, and reflects the pressures of the ecological and social mileu, which may differ greatly from one cetacean species to the next. The modulation of behavior or of behavioral interactions among animals that may accompany changes in ecology and sociality are discussed in the chapters by Norris and Dohl; Wells, Irvine, and Scott; Madsen and Herman; as well as in portions of the chapter on communication. Norris and Dohl discuss the organization of cetacean schools and their significance to cetacean life. Wells, Irvine, and Scott consider the variations in structure and social groupings that occur among inshore odontocete cetaceans, in the context of differences in resource distribution and predation pressure. Madsen and Herman focus on the visual adaptations of the cetaceans to their underwater photic environment and the functions that vision and visual appearance may serve in cetacean life. Much of the thrust of the chapter on communication is toward an understanding of the communication systems of the cetacean species as a response to the matrix of ecological and social pressures confronting them.

Although field studies of cetacean populations, oriented toward the analysis of behavior and social organization, are appearing with increasing frequency, thanks to the increased availability of support for this difficult but important

research, the cetacean maintained in the oceanarium or laboratory continues to provide the simplest point of access to the study of behavior. The chapter by Defran and Pryor reviews materials on behaviors of captive animals, and illustrates the variability in behavior and trainability that may be species-related. Commonalities in behaviors that may reflect convergent behavioral adaptations to similar ecological niches are briefly noted. The dolphin, usually meaning the ubiquitous bottlenosed dolphin *Tursiops* spp. or the common dolphin *Delphinus delphis*, has been a creature of myth and marvel throughout history. In very recent times popular interest has often centered on communication and cognition in the large-brained, vocal *Tursiops* spp. Given the limited number of scientific studies on these topics, free-wheeling speculation by press and public, and occasionally by the scientist himself, has often stepped into the gap of knowledge. The chapter on communication is in part an attempt to provide some firmer underpinnings for the understanding of cetacean communication and to relate it, where possible, to the attractive fabric of concepts created through the study of the communication systems of other, more accessible animals. The chapter on cognition describes the information-processing specializations, capabilities, and limitations of the dolphin, as revealed through laboratory studies of memory and conceptual abilities. The question of natural language is taken up here, as it is in the chapter on communication, and a distinction drawn between an extant natural language and the capability for acquiring some language fundamentals.

Most of the material in this volume is on the odontocete cetaceans, and much of that centered about the family of dolphins (Delphinidae). This is in keeping with the greater weight of behavioral data available for the delphinids, as compared with other cetacean groups. Some discussion of behavioral and social mechanisms and processes in the baleen whales (mysticete cetaceans) is to be found in several of the chapters, but, overall, the material is comparatively sparse. Field studies of the sociobiology of baleen whales are being actively pursued by many investigators today, so that knowledge of the behaviors of these animals and of their societies should expand greatly in the near future.

I wish to thank the contributors to this volume for their admirable patience with the editor, in what proved to be a longer-term undertaking than any of us had anticipated. The tragic loss in 1977, through theft and abandonment in the open ocean, of the dolphins Kea and Puka, with whom I had worked closely for many years, created an all-consuming burden that postponed work on this volume for well over a year. The postponement came at a time when much was happening in the cetacean field, so that, ironically, in the eventual resumption of work there was a greater scope to the material than might otherwise have been possible.

A number of reviewers commented on early versions of contributed chapters I sent to them. I am grateful for the time they gave to the task and appreciative of the wisdom of their comments. Reviewers included S. A. Altmann, Whitlow Au, George Barlow, Donald Dewsbury, A. D. G. Dral, William Evans,

Howard Gilliary, Sam Gruber, James McCormick, Keith Ronald, and William Stell. Additional reviewers solicited by the contributors themselves are acknowledged within each chapter.

There are many who offered support during the preparation of this volume, and by so doing made its completion easier, even possible. My wife, Hannah, has been many times a colleague in my studies and a counselor in my efforts. Her crisp intelligence helped me see more clearly through many a muddy issue, and her patience and understanding left me with energy to carry out the work. My good friends and research associates, Michael Yunker and Ronald Antinoja, provided invaluable assistance throughout much of the period of my work on this volume. Roger Thompson contributed insights and a great deal of hard work toward our research efforts during this same period. Among my current associates Paul Forestell was of continuous help and provided useful editorial comments on many of the chapters in this volume. Joe Mobley worked closely with me throughout the editorial process. His grasp of the material and of procedures made my work a lot easier. Douglas Richards and James Wolz, postdoctoral associates, commented helpfully on some of the material in this volume, and discussions with them have expanded my concepts and understanding of animal behavior. To the many other graduate and undergraduate students who helped in our research projects over the years, a fond Hawaiian *"Mahalo."*

Finally, the support of the National Science Foundation, Psychobiology Branch, for my research has been of fundamental importance in my efforts to learn more about cetacean behavior and has greatly facilitated the completion of this volume.

LOUIS M. HERMAN

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that were present in the terrestrial ancestors of the modern Cetacea. For example, new auditory pathways to the inner ear have been developed in the cetaceans because the mechanical ossicular system of terrestrial mammals, specialized as a matching network for overcoming the acoustic impedance differences between the external air medium and the fluid-filled inner air (van Bergeijk, 1967; Wever, 1974), is no longer suitable in the water medium. For humans, or other terrestrial mammals in water, the large impedance mismatch at the tympanic membrane junction of the fluid-filled external ear canal and the air-surrounded ossicular chain greatly reduces hearing sensitivity (Adolfson & Berghage, 1974). The development of echolocation in the toothed cetaceans has been accompanied by further changes in the hearing system, including enhanced frequency discrimination capabilities and high frequency hearing. These and related acoustic developments are treated further in discussions in this chapter. The reader is referred to other sources (e.g., Fleischer, 1976a; Norris, 1968; Reysenbach de Haan, 1957) for detailed discussions of the evolution of hearing mechanisms in the cetaceans.

Sound-production mechanisms have similarly undergone extensive adaptive changes in the cetaceans. The entire peripheral respiratory system has been greatly modified, not only to facilitate breathing, but as a sound-production mechanism. Special air sacs and valves have been developed that allow sound to be produced effectively without loss of air, and among the odontocetes, new structures for amplifying and beaming sound appear.

In the following sections the sound-producing, -detecting, and -analyzing systems of the cetaceans are discussed in greater detail. The material is principally restricted, however, to the family of dolphins, the delphinids, for which most information exists. Both structural and performance characteristics of the systems are described. Performance characteristics are expressed in terms of energy producing, detecting, or discriminating capabilities of the species, as estimated through physiological or psychophysical methods. In many cases, currently available data are insufficient to fully describe performance or to decide among hypothesized underlying mechanisms. Also, extrapolation of the findings on delphinids, primarily the bottlenosed dolphin *Tursiops truncatus*, to other cetaceans may not be valid. Crossing the line from odontocete cetacean to mysticete cetacean may be especially tenuous, and one may also expect that delphinid acoustic systems are very different from those described for pinnipeds or sirenids (cf. Bullock, Ridgway & Suga, 1971; Moore, 1975; Norris, 1968; Repenning, 1972; Reysenbach de Haan, 1957; Schusterman, Balliet & Nixon, 1972).

SOUNDS

Delphinid sounds are diverse and often complex (see Table 1.1). While a detailed review is beyond the scope of this chapter, a general overview of the

sounds and their associated behaviors is given to provide a context for the later discussion of acoustic mechanisms.

Sounds produced by odontocetes generally fall into two functional and three acoustic categories. The functional categories may be broadly defined as echolocation, in which the animal emits and detects its own sounds reflected from objects in the environment (see Griffin, 1968; Sales & Pye, 1974), and communication. The three acoustic categories describe the spectral composition, structure, or quality of the sounds and include the "creaky" buzzes, consisting of trains of generally broad-spectrum clicks associated with echolocation; the relatively pure-tone, often frequency-modulated (FM), whistles; and the burst-pulse sounds, also comprised of trains of clicks, but whose envelope gives a peculiar and variable "squawking," "blatting," "squeaking," or even "groaning" quality to the sounds. Some of the burst-pulse sounds may be produced by expelling air through the blowhole, but most seem to be generated internally without loss of air. Not all delphinids whistle (see Herman & Tavolga, this volume), but all seem to produce some forms of burst-pulse sounds. Whistles and burst-pulse sounds are most often implicated in communication.

Before considering these various sounds in greater detail, it is important to remind ourselves of some chronic problems in analysis that may limit the description and interpretation of sounds. One problem derives from the acoustical properties of the recording environment. Interfaces between water and other materials can significantly affect sounds by altering their duration, amplitude, or spectral characteristics (Parvulescu, 1964). Although tank and field studies may agree on the general nature of a sound produced by a particular species, the signal length and some aspects of the spectrum have been found to differ in the two situations (e.g., Busnel & Dziedzic, 1966; Norris, Evans & Turner, 1967; Norris & Evans, 1967). Whether this is wholly artifactual or at times indicative of adaptive changes made by the animals to maximize acoustic information is often not clear.

A second problem in analysis was stressed by Diercks, Trochta, and Evans (1973) in their discussion of how the recording system may alter the apparent characteristics of sounds, when that system has a narrower bandwidth than the sound under study. Diercks et al. contended that the echolocation clicks from certain delphinids may have been artifactually reported as narrow-band because the recording system itself was of narrow bandwidth. The spectral composition of the clicks in "narrow-band" species such as the harbor porpoise (*Phocoena phocoena*) may in fact be broad-band, similar to the clicks emitted by the bottlenosed dolphin and allied species. However, Watkins (1974) countered that narrow-band recording systems accurately represent the portion of the spectrum within the bandwidth of the system and that the apparent wide frequency range of harbor porpoise clicks reported by Diercks et al. (1973) may have resulted from hydrophone overload and noise in the system. The issue remains poised. While additional data by Møhl and Andersen (1973) and Dubrovskii, Krasov, and Titov (1971) indicate that harbor porpoise clicks may

indeed have energy up to 150 kHz, Ford and Fisher (1978), recording wild narwhals *Monodon monocerus,* have recently confirmed earlier work of Watkins, Schevill, and Ray (1971) that the clicks of these animals are very narrow-band. As Ford and Fisher noted, however, it still remains to be shown empirically that these clicks are used for echolocation.

Whistles and Burst-Pulse Sounds

Nonecholocating sounds produced by odontocete cetaceans have been given a wide variety of verbal labels by different workers. The energy in these sounds is often below 20 kHz, and in some mysticete species the energy may be as low as 20 Hz (e.g., Payne & Webb, 1971; Schevill, Watkins & Backus, 1964; Winn & Perkins, 1976). The whistle sounds are very narrow-band tones of continuous frequency (CF) or else are frequency varying. Harmonic components are normally present. The click structure of the burst-pulse sounds may be shifted in amplitude and/or rate, resulting in the variations of perceived sound quality described earlier as "squeaks," "squawks," and so on (cf. Lilly & Miller, 1961). The whole known acoustic repertoire of several delphinid species, including the killer whale (*Orcinus orca*), the Amazon River dolphin or "boutu" (*Inia geoffrensis*), and the harbor porpoise, consists of clicks produced at various rates (e.g., Busnel & Dziedzic, 1966; M. Caldwell, Caldwell & Evans, 1966; Evans, 1973; also see discussion in Herman & Tavolga, this volume).

Whistle sounds and burst-pulse sounds each vary greatly across or within animals of a given species (e.g., M. Caldwell & Caldwell, 1967; Dreher & Evans, 1964; Ford & Fisher, 1978). There may also be cases in which the sound production of individuals is highly stereotyped, especially for the whistles (Caldwell & Caldwell, 1968, 1971; but see discussion of whistle sounds in Herman & Tavolga, this volume). Caldwell and Caldwell (1968) hypothesized that the stereotyped character of the whistle of individual bottlenosed dolphins or of Pacific white-sided dolphins (*Lagenorhynchus obliquidens*) functioned as a "signature" to identify individuals within a school. Stereotype indicative of a possible signature function may also be found in the click "codas" of the sperm whale (*Physeter catodon*) (Backus & Schevill, 1966; Watkins & Schevill, 1977) or in the pulsing pure-tone sequences produced by the narwhal (Ford & Fisher, 1978).

A number of workers have attempted to catalog the sounds produced by individual delphinid species. A few examples can be given. Busnel and Dziedzic (1966) recorded a variety of sounds, including echolocation clicks, from a pilot whale (*Globicephala melaena*) at sea. The sounds included whistles up to 1 sec in duration with several harmonics, and a creak which appeared to be a rapid repetition of the echolocation click for 100 to 200 msec. In addition, there were a number of sounds combining various whistles and creaks, emitted simultaneously or sequentially. Recordings of the common dolphin (*Delphinus delphis*) by Busnel and Dziedzic (1966) revealed at least five types of sounds, each varying in frequency, FM, and harmonic components. Both whistles and

clicks were heard. There was considerably more FM within the whistle of the common dolphin than in the pilot whale.

The most extensively studied delphinid, the bottlenosed dolphin, produces a wide range of whistles and burst-pulse sounds. The burst-pulse sounds can be highly variable (e.g., M. Caldwell & Caldwell, 1967; Lilly & Miller, 1961). The whistles have few harmonics (Dreher & Evans, 1964; Evans & Prescott, 1962; Lilly & Miller, 1961) but may have FM components ranging from 4 to 20 kHz (Burdin, Reznik, Skornyakov & Chupakov, 1975; Evans & Prescott, 1962). Evans and Prescott (1962) observed 18 different whistle "contours" with durations from 0.10 to 3.6 sec and also identified a series of "barks" having energy from 0.2 to 16 kHz with abundant harmonics. Burdin et al. (1975) analyzed sounds of two Black Sea bottlenosed dolphins maintained in two separate tanks connected by hydrophones. The animals primarily used whistles during exchanges of vocalizations, with each animal using a different whistle. Similar results were reported earlier by Lang and Smith (1965).

Though all may agree that sound is an important channel in delphinid (and cetacean) communication (e.g., M. Caldwell & Caldwell, 1966, 1967, 1968; D. Caldwell & Caldwell, 1972, 1977; Dreher & Evans, 1964; Evans, 1967; Kinne, 1975; Lilly & Miller, 1961; Tavolga, 1965; Tavolga & Essapian, 1957; Titov & Tomilin, 1970), the correlations between sound and behavior are tenuous. The limitations in knowledge of dolphin acoustic communication contrast sharply with what is known about sound and its use in communication in many other animals, including insects, birds, and primates (for example, see papers in Busnel, 1963; Sales & Pye, 1974; Sebeok, 1968, 1977). The main problem in assessing delphinid acoustic communication is that in most cases, except for some oceanarium observations, it is difficult to correlate sounds detected with hydrophones with the specific animal making the sounds, much less with the behavior associated with the sounds (see, for example, Cummings & Thompson, 1971a). At sea the lack of suitable directional hydrophones makes it difficult to ensure that the observer is actually listening to the animal being observed visually unless the animals are close to the observers and the hydrophones, as during captures (e.g., Busnel & Dziedzic, 1966). Arrays of hydrophones help solve the directional problem, though they are expensive and often difficult to analyze (Watkins, 1976). An additional problem in interpreting the social value of sounds is that environmental and diurnal changes may as easily determine or modulate sound production as do social variables (Busnel & Dziedzic, 1966; M. Caldwell & Caldwell, 1967; M. Caldwell et al., 1966; Titov & Tomilin, 1970).

A few observations at sea have uncovered some tentative correlations between sound and behavior, although much remains to be done in all aspects of field observations. Playback studies at sea have demonstrated that the sound of several species may have dispersal effects on conspecifics and, in some cases, on other species. The whistle sound of a common dolphin recorded during capture increased activity by conspecifics for up to 15 min, while the same sound did not affect the behavior of schools of bottlenosed dolphins (Busnel & Dziedzic,

1968). The "screams" of the killer whale have a more general effect and elicited flight reactions or produced alerted states lasting long periods of time in several species of cetaceans (e.g., Cummings & Thompson, 1971b; Fish & Vania, 1971). However, the screams were ineffective in dispersing Pacific spotted dolphin schools (*Stenella atenuata*) in Hawaii, which have little or no experience with killer whales (J. Fish, personal communication). More recent field work, in which the fabric of the delphinid society is studied in great detail, as in the material reported in this volume by Norris and Dohl and by Wells, Irvine, and Scott provides the necessary context in which acoustic communication may be understood. It seems now that we are at a stage in the collection of descriptive information about cetacean sounds where it is of diminishing value to record and catalog without quantification or without taking firmer note of environmental and social correlates. Some questions that might be easily addressed include the effects of diurnal or seasonal changes on sound production in wild animals (cf. Powell, 1966), more work on the responses to conspecific and heterospecific sounds, and the ecology of sound production. Herman and Tavolga (this volume) have raised some of these same questions and others about cetacean acoustic communication and discuss them at greater length.

Echolocation Sounds

The echolocation sounds of most of the delphinid species studied are short, broadband pulses produced at a variable rate (Evans, 1973). All of the broadband types have energy extending into the ultrasonic region, though the degree of penetration may vary greatly across species. The possibility that the echolocation sounds of some species may be narrow-band (and of relatively low frequency) has already been noted. In addition to the variation in pulse characteristics across species, changes in pulse characteristics may also occur within species, depending on the echolocation task (e.g., Turner & Norris, 1966) or the environment (Au, Floyd, Penner & Murchison, 1974). Delphinid echolocation sounds may be contrasted with those of bats, which may be FM, or CF, or a combination of these two types (Diercks, 1972; Möhres, 1967; Novick, 1973; Pye, 1967; Sales & Pye, 1974; Simmons, Howell & Suga, 1975).

Interspecific differences in echolocation sounds mainly involve click length and frequency spectrum. Pulse duration in the bottlenosed dolphin is about 100 μsec, according to Diercks, Trochta, Greenlaw, and Evans (1971), who recorded from transducers attached to the animal's head, while Au et al. (1974) reported shorter pulse durations of 35 to 45 μsec in a long-range echolocation task in a high-noise environment (Fig. 1.1). Echolocation clicks in other delphinids are generally less than 1-msec long (see Table 1.1). The duration of killer whale clicks reported by Schevill and Watkins (1966) was 10 to 25 msec; however, Diercks et al. (1971), using a wide-band recording system, observed click durations of 0.5 to 1.5 msec in this same species. Whether or not the differences in click length may be artifactually derived from the different recording systems, as discussed earlier, is unresolved.
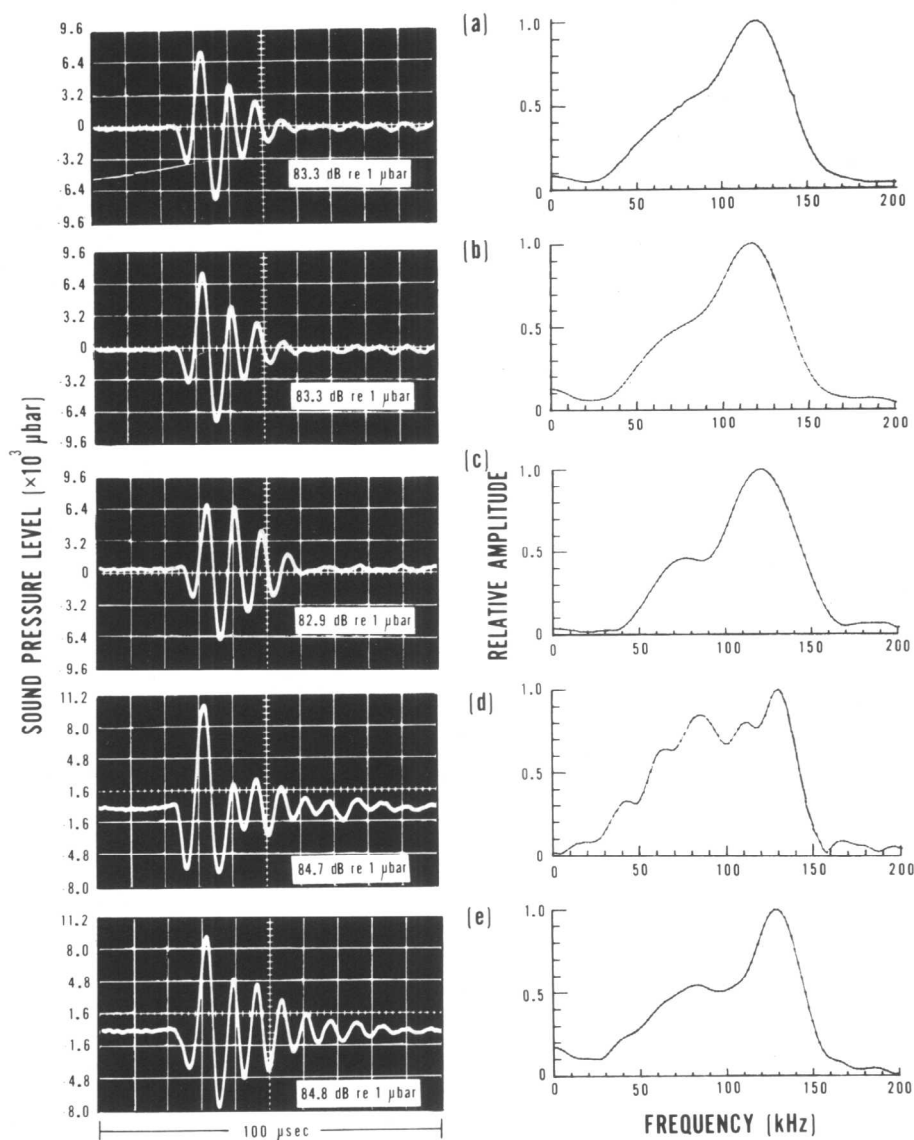
Fig. 1.1. Examples of some high-level echolocation clicks of *Tursiops truncatus* and their frequency spectra. The sounds were recorded in open waters during experiments on target discrimination, with the hydrophone placed 73.2 m from the test animal. From W. Au et al., *Journal of the Acoustical Society of America*, **56**(4) (1974), 1280–1290. Reproduced by permission.

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Table 1.1. Sound Emission Characteristics of Selected Odontocete Species

Species	Type of Sound	Frequency Range (kHz)	Maximum Energy (kHz)	SPL-dB re: 1 υbar (distance)	Signal Duration	Comments	Reference
Delphinus delphis	Click Whistles	4–16	4–9	45–80 (1 m)		Paired, clicks & whistles at same time 5 types of whistles	Busnel & Dziedic 1976
	Click	0.2–150	30–60	40–80 (1 m)			Gurevich, reported in Evans, 1973
Inia geoffrensis	Click	25–200	100			Single or multiple clicks	Norris et al., 1972
	Click				65 msec		Fish et al., 1976
Lagenorhynchus obliquidens	Click	0.06–80		70 (1 m)	0.25–1 msec		Evans, 1973
	Whistle	1–12			200–1200 msec	Data from 3 animals	M. Caldwell & Caldwell, 1971
Orcinus orca	Click Scream	0.25–0.5 2		60 (1 m)	10–25 msec	Multiple clicks	Schevill & Watkins, 1966
	Click	25	0.1–30	78 (1 m)	0.5–1.5 msec	Transducer on head tank	Diercks et al., 1971
	Click	to 35	12	80 (1 m)	0.1–0.5 msec	tank	Diercks, 1972

Species	Sound					Notes	Reference
Phocoena phocoena	Pulses	41	2	0 (1 m)	0.5–5 msec	Length depends on train cycle, limited recording system	Schevill et al., 1969
	Pulses	< 100–160	110–150	40 (1 m)	0.1 msec		Møhl & Andersen, 1973
Steno bredanensis	Click	0.1–200			50–250 μsec		Norris, 1969
	Whistle		3–10 2–14		100–900 msec		Evans, 1967
Tursiops truncatus	Click		120–130	80–85 (69 m) 128.6 (1 m)	35–45 μsec	Calculated at 1 m	Au et al., 1974
	Click	>octave	35				Diercks et al., 1971
	Click	0.2–150	30–60	40–80 (1 m)			Evans, 1973
	Click	0.1– >30			1–10 msec		Evans & Prescott 1962
	Bark	0.2–16			100 msec		
	Whistles	4–20			100–3600 msec	Narrow bands, 18 contours	
	Whistles	2–20			800–900 msec	Signature whistles, mostly pure tones	M. Caldwell & Caldwell, 1967
Stenella attenuata	Pulse	to 150			0.075–0.2 msec		Diercks, 1972
	Whistle						Evans, 1967

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For the Amazon bouto Table 1.1 shows that the spectral energy of the click lies entirely within the ultrasonic range (Evans, 1973; Dubrovskii et al., 1971; Møhl & Andersen, 1973). Other river dolphins, *Platanista gangetica* and *P. indi,* also produce very high-frequency components in the echolocation click, but there seem to be discrepancies in the literature as to whether sonic as well as ultrasonic components are also present (cf. Herald, Brownell, Frye, Morris, Evans, & Scott, 1969; Pilleri, Gihr, Purves, Zbinden & Kraus, 1976). Killer whale clicks, extending barely into the ultrasonic region, contrast strongly with the clicks of the river dolphins. Bottlenosed dolphin clicks generally have a rapid rise-time with spectral energy ranging from 0.2 to over 150 kHz (Evans, 1973). However, the major portion of the energy is concentrated in a relatively narrow band centered around 35 kHz in most circumstances (Diercks et al., 1971). Au et al. (1974) reported major energy between 120 to 130 kHz for two bottlenosed dolphins tested in an open-water, highly noisy environment. This dramatic increase in the location of the peak spectral energy of the clicks of the bottlenosed dolphins was interpreted as an adaptive response to masking background noise having significant energy in the 35-kHz region. Some of the variants in the clicks of different specimens of a given species may result from the different activities of the animals at the time when clicks were recorded (Ayrapet'yants & Konstantinov, 1974; Turner & Norris, 1966) or from changes in the position of the hydrophone relative to the head.

Source Levels

Delphinid echolocation sounds may contain a great deal of energy (Fish & Turl, 1976). Table 1.1 summarizes source level data, generally obtained at 1-m distance from the animal, for several species. Sound-pressure levels (SPL) for the killer whale (Diercks et al., 1971), harbor porpoise (Møhl & Andersen, 1973), and Pacific white-sided dolphin (*Lagenorhynchus obliquidens*) and common dolphin (*Delphinus delphis*) (Evans, 1973) range from 40 to 80 dB (re: 1 μbar).

The most impressive data on energy emission during echolocation was reported in the Au et al. (1974) study referred to earlier. SPL, measured at targets 65- to 75-m distance from two dolphins, were approximately 80 dB. Source levels derived from the theoretical transmission losses over these target distances were estimated to be 120 dB (re: 1 μbar) at 1 m from the two dolphins, with a peak level of 128.6 dB. Evans (1973) earlier reported source levels from bottlenosed dolphins of only 40 to 80 dB at 1 m, in an undescribed experimental situation, as did Fish and Turl (1976) in open-water conditions with relatively low background noise levels. The discrepancies in source levels of these different experiments are best viewed as reflecting the flexibility of response of the bottlenosed dolphin under various background noise conditions, even to the point, in the Au et al. study, of emphasizing portions of the audible spectrum—120 to 130 kHz—well outside the range of best auditory sensitivity (Johnson, 1966, 1967a), if more sensitive regions are preempted by noise.