



Bel'kovitch, V. M. and M. N. Sh'ekotov

The Belukha Whale: Natural Behavior and Bioacoustics

[Belukha. Povedenie i bioakustika v prirode]

Translated by Marina A. Svanidze

Edited by J. Christopher Haney and Cheri Recchia

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USSR Academy of Sciences
Shirshov Institute of Oceanology

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This translation follows as closely as possible the original meaning and intention of the Russian version. Errors in presentation, of omission or commission, published in the original may still be present in the translation. We have drawn attention to some of these by editorial comments in brackets using bold-face type. Additional errors are the sole responsibility of the translator and editors.

This book contains new original data concerning the behavior and bioacoustics of the belukha whale in natural environments, as well as data analysis of acoustic signals of the whales and methodological problems of ethological-acoustic research. This book is of interest to oceanologists, zoologists, ethologists, zoopsychologists, and bioacousticians.

Chief editor, M. M. Bel'kovitch

Abstract

This monograph presents new original material on the behavior and bioacoustic signals of the belukha whale in its natural environment. A typological classification of this species' signals is based on researches that were conducted for many years. This book as well contains descriptions of the time-frequency characteristics of the main classes of sounds. Comparison of the behavior and signals of the belukha whale synchronized by time, enabled development of an ethological-acoustical model of individual behavioral activity in search and hunting, and this study reveals the function of certain sounds. Also, the study made it possible to obtain data on the navigation mechanism (or orientation mechanism) and emphasizes the role of sounds in all the different behavioral activities of the belukha whale. Studies conducted at the extreme points of its range enabled, for the first time, comparison of the ethological-acoustic attributes of the belukha whale in the White Sea and the Amur River estuary.

Key words: belukha whale, white whale, *Delphinapterus leucas*, bioacoustics, Cetacea, animal communication

Foreward

The belukha whale (*Delphinapterus leucas* Pall., 1776) may reach a length of up to 5.5 m and weight of up to 1.5 tons. Up to now, the belukha is still rather numerous along the Arctic mainland, islands, and in the vicinity of river estuaries. It is well-known in Europe and America, where it has been kept for a considerable time in oceanariums and often takes part in circus performances.

The anatomical characteristics, geographic distribution, feeding, breeding, age and size parameters of the belukha whale have been described in numerous publications during the last 200 years. In 1964, Professor S. E. Kleinenberg and coauthors issued a summary "The belukha whale: a monograph of the species" that is up to now considered an outstanding work among all written about whales.

Thirty years ago, while working on this book, we did not yet know a lot about the acoustics of the belukha whale, except probably the fact that since ancient times fishermen and whalers used to call it "sea canary", due to twittering sounds that could be well-heard in boats. Also, the expression "to howl like a belukha" was widespread and originated from the belukha whale's behavior in extreme situations. However, this expression was often misattributed by many people to the fish (white sturgeon, *Huso huso*), large and delicious and better known than the Arctic white whale.

Knowledge of the behavior of the belukha whale was similar - it was accumulated through observations made by fishermen and captains for use in successfully hunting the whale, although this kind of hunting was always unstable due in particular to the belukha whale's quick adaptation to certain tools and methods of the hunting process.

These gaps in man's knowledge of the belukha whale's behavior and bioacoustics necessitated our systematic research on this subject. We began studies in the end of the 1970s in the White Sea, where we determined appropriate sites for observation of the belukha whale in its natural environment (the Summer Shore [Letniy Bereg] on Onega Bay). Data concerning the behavior and bioacoustics of belukhas were collected during times of intense hunting. Then these works were expanded towards the east to the Amur River estuary. The results obtained from these particular researches were analyzed and comprise this book.

Studies of the belukha whale's behavior and bioacoustics are continuing. At the present time, we are continuing to obtain data on ethological-acoustic characteristics of

belukha populations in Chukotka (Anadyr Bay) and, on the Sea of Okhotsk, studies of the belukha whale have begun. Thus, we managed to collect a uniquely complete library of belukha sounds that are synchronized by time in accordance with the whale's behavioral activity.

The analyzed materials enabled, for the first time, composition of the most complete "frequency glossary" of belukha signals; description of the signals in time-frequency models at a range up to 16 kHz; determination of which particular signals and how often belukha whales use them in different portions of the species range; and also preliminary direct and inverse correlations between acoustic signals and behavioral activities inherent to this species.

We would like to stress that all achievements were possible because of systematic research over many years - thousands of hours of observations, hundreds of hours of recordings, hundreds of photographs. Our methods of studying marine mammals in their natural environment reduced to a minimum signs of a researcher's presence, and allowed simultaneous reception of acoustic and visual data and their subsequent processing. These methods have been described in detail in previous publications (Bel'kovitch 1978, 1987).

Multi-year systematic observations not only gave us an opportunity to collect the most complete acoustic materials, but we could also watch the extreme plasticity in the belukha whale's behavior. For example, its searching and hunting behaviors in certain years were similar to the Black Sea porpoise (solo trawling of the sea bottom layer - "hunting by squares" in our terminology), and in other years more typical "caldrons", "carousels", or group hunting occurred.

In another example, we saw on the ocean surface only the white (or gray) portions of the belukha whale's dorsum rolling slowly from side to side. Only a few observers have succeeded in watching the entire whale in the ocean, typically while whales are lying motionless on the water's surface during sleep. It turned out that these whales were often sound asleep - repeated bumps by other whales' heads or tails did not wake sleeping whales. However, one very effective means of waking whales is when companions jump 3-4 m out of the water and splash water out of their mouths upon the head of the sleeping one.

The belukha whale is distributed throughout the severe climate of the Arctic, a fact that leads to interesting adaptative developments including those concerning its sonar system, signals, composition of flocks, and searching and hunting activities. Some of these matters are discussed in this book; others are still being analyzed or are expected to be explored in the future.

During the process of research, data collection and processing, we had the cooperation and support of the management of Shirshov Institute of Oceanology, in particular professor V.S. Yastrebob and corresponding member of the USSR Academy of Sciences M. E. Vinogradov, the chiefs of departments I. I. Tynyankin, A. L. Genkin, colleagues from IEMEG of the USSR Academy of Sciences - Professor V. A. Lemskiy, doctor of biology Romanenko, V.I. Markov, the director of the Acoustic Institute, Professor N. A. Dubrovskiy, colleagues from the Siberian branch of PINRO (Arkhangelsk), the director of candidates of biology V. A. Pot'elov, and candidate of biology Yu. K. Timoshenko. The large and fruitful work in these studies was done by all the staff of the Marine Bioacoustic Laboratory of the Shirshov Institute of Oceanology of the USSR Academy of Sciences. An important participation in preparing illustrations were done by A. V. Agabonov and candidate of biology G. A. Boyko. Gratitude to all.

Doctor of biology,

V. Bel'kovitch

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Chapter 1. A brief review of acoustic signals of cetaceans.

A large amount of data from research on cetacean sounds has been obtained, and the number of such studies continues to grow. Until the 1940s, there were only sporadic descriptions of whale sounds, often recorded primarily in air (Lindholm 1888, Rawitz 1899, 1900, and others). Later, some descriptions of dolphins' sounds were made in captivity (Tomilin 1957, McBride and Hebb 1948, Wood 1952, and others). Only since the 1950s have tape recordings of whales' "voices" been analyzed (Schevill and Lawrence 1949, 1950, Kellogg 1953, 1961, Evans and Prescott 1962, and others).

Today, all researchers agree that whale sounds play an important role in orientation and are used in communication. Minding the purpose of this review, we pay most attention to systematic generalizations of accumulated data. The problems concerning communication and orientation need specific attention, thus they are mentioned and described only in general to outline the whole problem. It is worthwhile to note that communication signals carry information important for navigation, stating location, behavior character of the source, allowing its identification and so on. Evidently, another factor is true as well: location signals given by one of the animals to others contain certain additional information about the character of its behavioral activity. So, due to their physical nature, all the acoustic signals are polyfunctional although still specialized.

Before we begin this review, it is necessary to note that cetaceans produce lots of sounds that by hearing can be characterized as "roar", "groan", "sigh" (deep breath), "mooing", "squeal", "crack", "trill", "whistle", "squeak", "buzz", "blow", "shot", and so on. Today, the fact that all cetaceans produce sounds is considered to be entirely determined, although the level of studies varies within different families and genera.

1. Suborder: (Mysticeti Flower, 1864)

A. Family: right whales (Balaenidae Gray, 1825)

Genus: (*Balaena* Linnaeus, 1758)

bowhead whale (*Balaena mysticetus* Linnaeus, 1758)

Bowhead whales produce very loud sounds of breathing than can be heard at distance of a mile (Lepekhnin 1905). This sound is of low frequency, and corresponds to the exhaled breath. According to tape recordings made in the Arctic (Poulter 1966, 1968, 1971), submarine acoustic signals of the bowhead whale are represented by low-frequency and narrowband cries of duration 1-2 sec. More detailed analysis of these sounds was made difficult by the fact that they were obtained along with the sounds of a seal, and Poulter (1971) considered that the signals of these two species were similar. Thus, the seal's signals could interfere with the the whale's signals and as a result modify the spectral

picture. Bowhead whales, squeezed by ice, produced "clicks" that were recorded with the help of a stethoscope (Beamish 1974).

Genus: southern right whales (*Eubalaena* Gray, 1864)

northern right whale (*Eubalaena glacialis glacialis*, 1781)

In air, northern right whales produce muted metallic sounds (Matthews 1938) and "moo" when wounded. The acoustic signals of the northern right whale were the first to be recorded. They were low-frequency "groans" and "howls" in the frequency range up to 0.4 kHz (Schevill and Watkins 1962, Payne and Payne 1971, Cummings et al. 1972), probably of coherent character. The use of a broadband (up to 150 kHz) recording device did not reveal pulsed signals suitable for echolocation in this species. Additional sounds concerned feeding in the upper layers (Watkins and Schevill 1976) and probably were of communicative significance.

In Newfoundland, Cummings and Phillippi (1970) recorded repeated signals ("stanzas") of 11-14 min duration, composed of short pulses ("blips") and "screams" at frequencies of 20-175 Hz. Payne and Payne (1972) did not discover such "stanzas", but they used a recording device with a low-frequency limit of over 175 Hz, and thus were unable to record such low-frequency sounds. However, the known signals of both bowhead and northern right whales are similar (Schevill and Watkins 1962) and do not contain "stanzas" as in the humpback whale. [Complicated signal systems in the humpback whale occur only in tropical waters in the period of December-April, although one should not exclude the opportunity to hear a wide spectrum of different signals in this region of its range (Payne and McVay 1971, Winn et al. 1970a, Winn and Winn 1978). However, near Newfoundland at the end of December they also can produce sounds while preparing to migrate south.] Nevertheless, there is as yet no direct proof that northern right whales do not "sing". Long-term research studies of the species' bioacoustics are necessary.

southern right whale (*Eubalaena glacialis australis*)

Concentrations of this species along the shores of Patagonia, where they come for breeding (Nuevo San Jose Bay; Gilmore 1969, Cummings et al. 1972, Payne and Payne 1971) contributed to studying its signals in conditions ideal for observation, and enabled observation and recording of signals with the possibility of correlating acoustics with behavior (Fish and Thompson 1972, Payne 1972). The most common sound is a "belch" of 0.9-2.2 sec duration (mean 1.4 sec), with the main energy at a frequency of 235 Hz and a frequency range of 30-2200 Hz (the majority to 500 Hz). "Screams" (and "mooring") were a second type of sound. Single "moos" had durations of 0.6-1.6 sec in a narrow frequency range of 70-320 Hz (fundamental 160 Hz). Complex "moos" had harmonics and were of longer duration, wider frequency range (between 30 and 1250 Hz,

fundamental 235 Hz), and duration 0.2-4.1 sec. Pulsed signals in a frequency range of 20-2100 Hz and of 60 msec duration were noticed often with "mooing" at the same time. Correlation of acoustic signals with time of day was not discovered. "Stanzas" that could be explained by differences in season, environment, geography, or populations were not discovered. Signals of *Eubalaena glacialis australis* during the breeding period were common. The "belch" sounds were heard more seldom and were substituted with "moos" and "screams" (by recorded frequencies) of more intensity. On the basis of 1750 sounds analyzed, the great majority of signals are similar to those produced by humpback whales (Watkins 1967), except strong "blasts" at 50-2200 Hz and also sounds of breathing.

Signals of *Eubalaena glacialis australis* (Payne and Payne 1971, Payne 1972) are similar in general to those known from the northern right whale. It was discovered that about two signals per hour were usually produced during daytime, but at night acoustic activity increased sharply (60-900 signals per hour). Frequencies were in the 50-500 Hz range; it is rare to record high-energy signals of greater than 1500 Hz.

More recent research on the signals of southern right whales not only singles out a number of types, but in certain cases it has also been possible to determine their functional significance (Clark 1983). This author identified the following classes of acoustic signals: 1) "up calls" - low frequency tonal sounds of increasing frequency of 50 Hz to 200 Hz and duration 0.5-1.5 sec; 2) "down calls" - low-frequency tonal sounds of decreasing frequency of 200 Hz to 100 Hz and duration 0.5-1.5 sec; 3) "constant calls" - tonal signals of this class have almost constant dominant frequency in the range of 50-500 Hz and 0.5-6 sec duration; 4) "high calls" - key signals of 200-500 Hz with duration 0.5-2.5 sec, often ended with rapid frequency decreases; 5) "hybrid calls" - complex signals that begin like "high calls" but become pulsive at the end, with dominant frequency of 50-500 Hz, duration 0.5-2.5 sec; 6) "pulsive calls" - complex, usually harsh, amplitude-modulated sounds that continue for 0.5-3.5 sec at 50-200 Hz; 7) "blows" - noisy broadband sounds of frequency 100-400 Hz and duration of up to 26 sec; 8) "slaps" - short, broadband signals with dominant frequency of 50-1000 Hz and duration 0.2 sec. Single whales typically produce signals of the first class. Excited female whales exchange signals of the fourth class. In a group of excited animals (mating behavior), signals of the fourth, fifth, sixth, seventh, and eighth classes were common.

B. Family: (Balaenopteridae Gray, 1864)

Genus: rorqual whales (*Balaenoptera* Lacepede, 1804)

blue whale (*Balaenoptera musculus* Linnaeus, 1758)

Whalers knew rather monotonous sounds of breathing in this species, resembling loud groans (Millais 1906). Series of signals of 523 Hz and 37 sec duration were recorded that

repeated regularly every 100 sec. The signals spread out over 170 km and are evidently used for communication (Anonymous 1970).

Recently, new data have been obtained on the pulsed signals of the blue whale. "Clicks" and groups of clicks were recorded at a maximum frequency of 8 kHz (Poulter 1968). In addition, recordings of typical echolocation signals were made (Beamish and Mitchell 1971) that had frequencies in the range up to 31 kHz (intensity maxima of 6 and 25 kHz), durations of 0.5-1.0 msec, and maximum recurrent frequency 442 pulses per second. A total of 5000 clicks of feeding whales were recorded. Due to their physical characteristics, these signals of rather great power (159 dB re $1\mu\text{Pa}/1\text{ m}$) could be used to find prey and correlate with nutritional mode (stenophagia) in this species. The authors supposed that these signals are used to detect zooplankton.

On 30 and 31 May 1970 at Guafo Island, Chile, sounds of 2-4 whales of this particular species were recorded. The recording device had a frequency range of 25 Hz-18 kHz (± 5 dB). The change in amplitude of the signals correlated with the movement of the whales. According to four estimates of intensity, the average meaning source level was 188 dB re $1\mu\text{Pa}/1\text{ m}$.

Low-frequency and frequency-modulated cries in the 12-200 Hz range were of average duration 36.5 sec (range 34.7-38.1 sec). They consisted of A, B and C parts, different by 4M degree. The signals of two whales had intervals between B and C, and in one whale between A and B. Part A (frequency 390 Hz and duration 0.5-1.0 sec) always (27 signals) preceded part C. The strongest energy of all three parts of the cry was at 20, 25, and 31.5 Hz. The interval between B and C was constant and averaged 100 and 106 sec (two whales), but its duration was correlated with the breathing cycle: exhaling on the surface (Cummings and Thompson 1971a,b).

It is known that along the Chilean coast, blue whales produce 20 Hz sounds. During the same season, long multi-component signals of the species typify blue whales occurring in the northeast Pacific Ocean, thus giving evidence of geographic variation (Thompson et al. 1979). More recent studies showed that low-frequency long pulses of blue whales in Hawaii differ from sounds recorded in this species along the Chilean coast (Thompson and Friedl 1982).

Various kinds of groans are produced by blue whales: simple (average dominant frequency of 90 Hz that can reach 158-179 Hz) and compound sounds (with additional pulses of 20-2000 Hz, duration about 1 sec) have been noted by a number of researchers (Ljungblad et al. 1980, 1982, Edds 1982). Some blows of sharp-impulse, broadband sounds were recorded during spring migrations (Clark and Johnson 1984). The frequencies were 100-3500 Hz, and signal durations varied from 0.3-0.7 sec. Intensity

levels were 175-185 dB re 1 μ Pa/1 m (Würsig et al. 1982). In spring, blue whales produce unique song-like consecutive sounds consisting of combinations of 2-3 tones as well as signals similar to the elephant's trumpet sounds; these have dominant frequencies up to 5 kHz (Ljungblad et al. 1982).

Studies of signals produced by blue whales along the Alaskan coast revealed groans of 25-900 Hz and songs recurring up to 20 times at 20-5000 Hz frequency (Cummings and Holliday 1987). The intensity maximum was 189 dB (1 μ Pa/1 m). The whales produced more signals in the morning (6-8 a.m.) and at night (4-6 p.m.).

A blue whale found trapped in drifting ice produced 7 series of short, sharp pulses during 3 hours; the number of pulses in a series varied from 7 to 27. The duration of inter-pulse intervals also changed, being on average 15-21 msec (Beamish 1979). The signals were recorded by three hydrophones simultaneously; the author succeeded in showing that high-frequency signals were sent through the water off the forward part of the head.

fin whale (Balaenoptera physalus Linnaeus, 1758)

After the blue whale, this is the largest animal in the world. Pulsed signals recorded in the North Atlantic and in the Pacific Ocean have been ascribed to fin whales (Schevill et al. 1964). These signals were of frequency 20 Hz and duration 1 sec, and were produced with regular intervals several times per minute for many hours. The seasonal character of these signals, the distribution of signal sources (1 per 300 square miles), "aimless" movement at a speed of 3-5 km per hour (up to 12 km per hour), and low frequency and wattage (1-25 watts) all give credence to the idea that the signals originate from fin whales. Schevill et al. (1964) give persuasive evidence for specific identification. The breaks in signals may have related to the whale's appearance at the ocean surface. Later studies showed that sounds called "20 Hz signals" actually varied in frequency. Presumably these sounds spread for hundreds of miles (Payne and Webb 1971). However, at an intensity of 170-185 dB (re 1 μ Pa/1 m), noise that hydrophone cables emit may strongly influence the estimate (Walker 1963). Accordingly, careful hydrophone placement is necessary to obtain more precise results.

These signals may be produced in pairs. Such doubled sounds have typical features, e.g., a doubled sound "22-15" sec (Patterson and Hamilton 1964). This refers to a 22 sec interval between the sounds and 15 sec interpulse interval with pulse duration about 1 sec. In some of the whale cases, a difference in main frequencies of pulses was observed. Pulses of the following frequencies were recorded: 17, 18.5, 19, 20, and 40 Hz, all of which were useful in individual identification, although it is doubtful that whales can distinguish between differences of 1 Hz. Echolocation signals of fin whales were recorded at 20 yards distance from the ship (Wright 1962); these signals had frequencies of 20-39

kHz. (These signals may have originated rather from sperm whales). Series of pulses (clicks) originating from two fin whales at 16-28 kHz were recorded at 50 yards from the ship. Each pulse consisted of 3-4 parts that had durations of 3-4.4 msec, inter-pulse intervals of 250-336 msec, and durations for the whole series of 8.8 sec (Thompson et al. 1979). Signals produced by two fin whales (125 miles off Bermuda) sounded like whistles of 1.5-2 kHz (up to 5 kHz) and had durations of 50-600 msec (Perkins 1966). The author classified the sounds as "signals of alarm". However, although fin whales occur there, these signals sounded very similar to whistles of sei whales in their wintering range. These signals are worthy of further study. They have not been mentioned in later publications (Watkins 1981) in which fin whale signals and corresponding behaviors were analyzed in great detail. That author found communicative "high frequency sounds" with durations of about 0.3 sec and 0.1-30 kHz frequency. Certain pulses and "20 Hz" series concerned sexual behavior. "Ragged LF pulses" had frequencies lower than 30 kHz, and pulse durations of 0.1-1.0 sec. The following class of signals, "LF rumble", were used to demonstrate surprise or aggression; this class of signals had frequencies less than 30 kHz as well. Pulsed signals of fin whales were also recorded and concerned feeding on the ocean surface.

Bryde's whale (*Balaenoptera edeni* Anderson, 1878)

This species is common to warm waters between 40° north and 40° south latitude (Nishiwaki 1972). When compared to other species of this family, the distinguishing feature is three ridges along the dorsal portion of the snout, but from a distance it is difficult to distinguish from sei and fin whales.

Along the Mexican coast, 288 cries were recorded (± 5 dB, 25 Hz-18 kHz) originating from one or two whales identified by underwater photography (Thompson and Cummings 1969). The signals varied in frequency and duration. Analysis of 23 signals showed that they occurred at 20-245 Hz with durations of 0.2-1.5 sec (average 0.42 sec). The signals were produced sporadically at intervals of 0.2-9 minutes. Frequency modulation was on average 15.2 Hz up and down. The same day, 35 cries were recorded belonging to another individual, similar to preceding ones, although with average frequency 132 Hz and average duration 0.4 sec.

In California Bay, low frequency "groans" were successfully recorded in June. These signals had an average duration of 0.42 sec and frequency of 124 Hz, but 73% of the signals had whistling sounds with increasing and decreasing frequencies (Cummings et al. 1986). In the southern Atlantic Ocean (30° 07', 14° 55'), click series belonging to Bryde's whale were recorded, similar in sound to those of the minke whale (Beamish and Mitchell 1973).

sei whale (*Balaenoptera borealis* Lesson, 1828)

This species is little-known from acoustic records; it may easily be confused with fin and Bryde's whales. In air, sei whales produce a loud whistle emanated from the throat and having a sharp sound like a metallic stroke (Tomilin 1957). In the region between Nova Scotia and Newfoundland (44° 49', 56° 28'), where a few individuals occurred close to the ship, click series were recorded (recording bandwidth 50-7500 Hz) with maximum energy at 3 kHz; the total duration of a series was 7 sec while the duration of a single click was 4 msec. "20 Hz signals" were recorded as well, but were concealed by cable noise. When common dolphins approached the recording site, low frequency clicks were recorded, but the above-mentioned click series are not known from dolphins (Busnel and Dziedzic 1966).

minke whale (*Balaenoptera acutorostrata* Lacepede, 1804)

With its sharply-shaped head, this is the smallest member of the genus *Balaenoptera* (maximum length is 10.2 m; Nishiwaki 1966a), inhabiting all oceanic zones from polar regions to tropical seas. In air, loud sounds of exhaling ("groans") were heard, similar to those of the fin whale (Tomilin 1955, 1957). Schevill and Watkins (1972) were the first to report low frequency sounds of minke whales in the polynya off Ross Land, Antarctica (recording device bandwidth 30 Hz-30 kHz). During these signals, frequencies declined from 130-115 Hz to 60 Hz. Sound intensity was 165 dB (re 1 μ Pa/1 m), and sound duration was 0.2-0.3 sec with intervals of 8-97 sec.

Low-frequency "screams" were recorded at different frequencies from 80 to 140 Hz and durations of 165-320 msec (Winn and Perkins 1976). In frequency and duration these "screams" were similar to those recorded earlier (Schevill and Watkins 1972), but they were produced in series of regular and irregular intervals with a repetition rate of 2.1-2.3 pulses per second. The majority of minke whale sounds were organized into "series", sources long ago recorded in the ocean as A-series. The frequency of these signals is of changeable nature and may reach more than 800 Hz (most between 100 and 200 Hz), although according to other notes, the energy minimum is 2 kHz. Individual variations of such signals by duration are 50-70 msec with rather stable consecutive frequency, and total duration of the series is more than 1 min. These signals are of individual character (Thompson 1979), similar to differences in frequencies of sound composition and recurrence among species.

Short series and clicks are divided into several groups according to dominant frequency (Winn and Perkins 1976): 1) 3.3-3.8 kHz; 2) 5.5-7.2 kHz; 3) 10.2-12.0 kHz, of 0.5-1 msec duration. "Ratchet-like" pulses had a maximum frequency of 850 Hz, duration of 1-6 msec in the case of single pulses and 25-30 msec for groups of pulses.

Genus: humpback whales (*Megaptera* Gray, 1846)

humpback whale (*Megaptera novaeangliae* Borowski, 1781)

In air, sounds produced by humpback whales used to be compared with steam locomotive horns (Rawitz 1900, Tomilin 1955). Watkins (1967) described an unusual signal - an exhalation with whistling. This sound, with a frequency of up to 2 kHz and duration 2 sec, is evidently produced when exhaling and can be heard both underwater and in air. These sounds are supposed to be produced arbitrarily and are clearly different from those produced during normal exhaling. The noises sound much louder in air (by 35 dB) than the typical sound of exhaling. Underwater, the sounds were of higher frequencies than normal exhalations, but of the same intensity level.

A large number of publications from the years 1949-1955 refer to underwater sounds of the humpback whale, but it was not until 1962 that spectrograms of underwater low-frequency signals of this species were first published (Schevill and Watkins 1962). Tavolga (1968) described some of them, e.g., cries of 150-800 Hz of 1-1.5 sec duration, and cries of 2 kHz of 0.5 sec duration. As well, higher frequency cries of 4-8 kHz were mentioned (Levenson 1969, 1972). The most typical were "low grunts" at 120-250 Hz and "squalls", whistles, and "wailing turkey-like" sounds of dominant frequency of 0.5-1.65 kHz. The level of the sounds was 124.4-155.4 dB (re 1 μ Pa/1 m).

As defined recently, humpback whales are the most vocal whale species. In tropical waters during winter, complex and compound sounds including recurrent "songs" change constantly (Payne et al. 1983). The most obvious changes are when other individuals join in the group choruses. It was discovered that humpback whales "sing" (Winn et al. 1973, Tyack 1980, 1981, Darling et al. 1983, Glockner 1983). Each "singing" whale changes its "song" in accordance with other members of its group (Guinee et al. 1983). Humpback "songs" can be characterized as recurrent series of sounds of common frequency lower than 4 kHz (Anonymous 1969, Payne and McVay 1971). They contain several acoustic themes, consisting of phrases or syllables (units according to Payne and McVay 1971). Themes and phrases sound in strict order and are repeated monotonously. The song may last for 7-36 min, but always has strictly organized structure. The difference in duration depends on the number of phrases or changes of each theme (Thompson and Winn 1977). Coming to the surface terminates the song, but after diving the song begins immediately once again. The song of humpback whales differs from bird song in terms of structure and song interval. On the whole, the character of the song (according to differences in sounds and phrase compositions) is in some way specific for mating and inter-generational transfer (with some individual variations).

The analysis of dialects (Winn and Winn 1978) of different populations hardly allows distinguishing types of songs due to inadequate material and annual changes in song fragments (Winn and Winn 1978, Payne and Payne 1979). However, differences exist in fragments and distinctive dialects probably occur among populations. For example, song phrases off New Zealand, Hawaii, and California do not sound similar to those from the northwestern Atlantic Ocean (Thompson et al. 1979). The major differences are between humpback whale songs recorded in the northern Pacific and the northern Atlantic oceans, although the basic structure of the "songs" has similar features (Payne and Guinee 1983). Studies of sounds of humpback whales in the Hawaiian Islands also identified atypical "songs", that formed from typical ones in natural and predictable ways (Frumhoff 1983). Some researchers offer an unusual interpretation of the functional meaning of humpback whale song as an indication of the male's physical condition, advertising length of time spent underwater (Chu and Harcourt 1986).

Besides songs, clicks at frequencies of 2-7 kHz, and noise signals emanated by non-singing whales were produced (Winn et al. 1970a). Analysis of signals originating from a stranded whale near Newfoundland showed diversity, irregularity, and absence of song-like organization (Winn and Winn 1978).

Rather recently, an attempt was undertaken to discover the acoustic signals of humpback whales in their summer feeding regions in southeastern Alaskan waters (Thompson et al. 1986). Underwater signals of whales comprised mainly "groans" (20-1800 Hz), "grunts" (25-1900 Hz), "piercing moans" (0.4-2 kHz), recurrent pulses (25-80 Hz) and strikes on the surface. The "groans" contained harmonic sounds and could be subdivided into simple and complicated ones of average duration 800 msec. Most of the "groans" had slight frequency modulation. The "grunts" did not have any harmonic structure; they had a pulsed nature with increasing frequency modulation. Repetition rates of 850 "groans" and "grunts" were 1.8-3.2 sounds per minute. "Moans" (piercing and trumpet-like) had a plain harmonic structure and 400-600 msec duration.

The duration of low-frequency pulses out of distinctive sequences varied from 300-400 msec. Some of these pulse emanations had tonal characteristics, sometimes harmonized. The average frequency of emanations in repeated sequences was 5 times per min (duration of recording - 8.5 hours). All of the low-frequency pulse emanations were accompanied by unspecific enlargement of noise spectrum (40-1250 Hz) that as a rule decreased in intensity with duration. The authors attribute the pulses to generation of air bubbles when whales make spiral maneuvers during bubble-net feeding (for more details see: Wolman 1978, Earle 1979, Payne 1979). The accompanying noise (40-1250 Hz) was the result of air bubbles rising toward the ocean surface.

Many "non-singing" sounds belonging to this species turned out to be closely connected with social interactions, in particular with the demonstration of aggressiveness and the state of excitement in groups of whales near the Hawaiian Islands (Silber 1986). The majority of such aggressive interactions are inherent to males (Baker and Herman 1984). Sounds recorded by Silber were of duration 0.25-5 sec and in a frequency range up to 10 kHz, although the dominant frequency of most signals was not higher than 2 kHz. An increase in the size of the group caused an increase in the level of emanating signals. Humpback whales "sing" during migrations as well, their calls serving as indicators of migratory routes (Kibblewhite et al. 1967, Levenson and Leapley 1978, Mattila et al. 1987, Stone et al. 1987, Clapham and Mattila 1990).

C. Family: gray whales (*Eschrichtiidae* Ellerman et Morrison-Scott, 1981)

Genus: gray whales (*Eschrichtius* Gray, 1864)

gray whale (*Eschrichtius gibbosus* Erxleben, 1877)

The gray whale's signals in air are exhaled breaths with inherent strong bass sounds. Signals were recorded at the 40-400 Hz range with energy maximum at 80-300 Hz (Eberhardt and Evans 1962). Each signal continued for about 0.1 sec and consisted of 4-5 emanations. Neither whistles nor clicks were recorded. Schevill (1964) discovered whistles during mating activity of the gray whale, but did not record such sounds during feeding.

Gray whale signals recorded in the sea showed that the most typical "groaning" sounds occur at 20-200 Hz with a duration of 1.5 sec (Cummings et al. 1968). "Whistling" signals with duration 1.25 sec occur in the range of 15-175 Hz; "gurgling" signals are more rare and occur in the range of 15-305 Hz with duration 0.7 sec. "Striking sounds" were as well noted at 350 Hz. The intensity of these signals is 132-152 dB (re 1 μ Pa/1 m). All these signals were recorded in all seasons of the year and it is still impossible to identify them with respect to particular kinds of gray whale activity.

Originally, some researchers denied the fact that these whales produce echolocation signals (Rasmussen and Heed 1965). Later, echolocation clicks were discovered in the frequency range of 70-3000 Hz (maximum energy at 400-800 Hz). These sounds had durations of 10-15 msec, with an interval between pulses of 150-350 msec, and were reminiscent of sounds originating when rubbing the teeth of a comb (Asa-Dorian and Perkins 1967). A young gray whale (named Gigi) produced signals that sounded like "metallic pulsating signals", and resulted from human touches of the mammal's head. Signals consisted of 8-14 impulses with duration of 2 sec and frequencies from 100 Hz to above 10 kHz with energy maximum at 1.4 kHz. This signal was produced more than 5

