

Cetacean Acoustics

20. Cetacean Acoustics

The mammalian order cetacea consist of dolphins and whales, animals that are found in all the oceans and seas of the world. A few species even inhabit fresh water lakes and rivers. A list of 80 species of cetaceans in a convenient table is presented by *Ridgway* [20.1]. These mammals vary considerably in size, from the largest living mammal, the large blue whale (*balaenoptera musculus*), to the very small harbor porpoise (*phocoena phocoena*) and Commerson's dolphin (*cephalorhynchus commersonnii*), which are typically slightly over a meter in length.

Cetaceans are subdivided into two suborders, odontoceti and mysticeti. Odontocetes are the toothed whales and dolphins, the largest being the sperm whale (*physeter catodon*), followed by the Baird's beaked whale (*berardius bairdii*) and the killer whale (*orcinus orca*). Within the suborder odontoceti there are four superfamilies: *platanistoidea*, *delphinoidea*, *ziphioidea*, and *physeteridea*. Over half of all cetaceans belong to the superfamily *delphinoidea*, consisting of seven species of medium whales and 35 species of small whales also known as dolphins and porpoises [20.1]. Dolphins generally have a sickle-shaped dorsal fin, conical teeth, and a long rostrum. Porpoises have a more triangular dorsal fin, more spade-shaped teeth, and a much shorter rostrum [20.1].

Mysticetes are toothless, and in the place of teeth they have rigid brush-like whalebone plate material called baleen hanging from their upper jaw. The baleen is used to strain shrimp, krill, micronekton, and zooplankton. All the great whales are mysticetes or baleen whales and all are quite large. The sperm and Baird's beaked whales are the only odontocetes that are larger than the smaller mysticetes such as Minke whales and pygmy right whales. Baleen whales are subdivided into four families, *balaenidae* (right and bowhead whales), *eschrichtiidae* (gray whales), *balaenopteridae* (Minke, sei, Bryde's, blue, fin, and humpback whales), and *neobalaenidae* (pygmy right whale).

Acoustics play a large role in the lives of cetaceans since sound travels underwater better than any other form of energy. Vision underwater is limited to tens of meters under the best conditions and less than a fraction of a meter in turbid and murky waters. Visibility is also limited by the lack of light at great depths during the day and at almost any depth on a moonless night. Sounds are used by marine mammals for myriad reasons such as group cohesion, group coordination, communications, mate selection, navigation and locating food. Sound is also used over different spatial scales from tens of km for some species and tens of meters for other species, emphasizing the fact that different species utilize sound in different ways. All odontocetes seem to have the capability to echolocate, while mysticetes do not echolocate except in a very broad sense, such as listening to their sound bouncing off the bottom, sea mounts, underwater canyon walls, and other large objects.

The general rule of thumb is that larger animals tend to emit lower-frequency sounds and the frequency range utilized by a specific species may be dictated more from anatomical constraints than any other factors. If resonance is involved with sound production, then anatomical dimensions become critical, that is, larger volumes resonate at lower frequencies than smaller volumes. The use of a particular frequency band will also have implications as to the distance other animals, including conspecifics, will be able to hear the sounds. Acoustic energy is lost in the propagation process by geometric spreading and absorption. Absorption losses are frequency dependent, increasing with frequency. Therefore, the sounds of baleen whales such as the blue whale that emit sounds with fundamental frequencies as low as 15 Hz can propagate to much longer distances than the whistles of dolphins that contain frequencies between 5 and 25 kHz.

20.1	Hearing in Cetaceans	806
20.1.1	Hearing Sensitivity of Odontocetes	807

20.1.2	Directional Hearing in Dolphins ..	808	20.3	Odontocete Acoustic Communication	821
20.1.3	Hearing by Mysticetes	812	20.3.1	Social Acoustic Signals	821
20.2	Echolocation Signals	813	20.3.2	Signal Design Characteristics	823
20.2.1	Echolocation Signals of Dolphins that also Whistle	813	20.4	Acoustic Signals of Mysticetes	827
20.2.2	Echolocation Signals of Smaller Odontocetes that Do not Whistle .	817	20.4.1	Songs of Mysticete Whales	827
20.2.3	Transmission Beam Pattern	819	20.5	Discussion	830
			References		831

20.1 Hearing in Cetaceans

One of the obvious adaptations for life in the sea is the absence of a pinna in cetaceans. The pinna probably disappeared through a natural selection process because it would obstruct the flow of water of a swimming animal and therefore be a source of noise. In the place of a pinna, there is a pin-hole on the surface of a dolphin's head which leads to a ligament inside the head, essentially rendering the pinna nonfunctional in conducting sounds to the middle ear. So, how does sounds enter into the heads of cetacean? Several electrophysiological experiments have been performed in which a hydrophone is held at different locations on an animal's head and the electrophysiological thresholds are determined as a function of the position of the hydrophone [20.2–4]. All three studies revealed greatest sensitivity on the dolphin's lower jaw.

The experimental configuration of Møhl et al. [20.2] is shown in Fig. 20.1a, which shows a *suction-cup* hy-

drophone and attached a bottlenose dolphin's lower jaw and the surface contact electrodes embedded in suction cups used to measure the auditory brainstem potential signals for different levels of sound intensity. The important differences in the experiment of Møhl et al. [20.2] are that the subject was trained and the measurements were done in air so that the sounds were limited to the immediate area where they were applied. The results of the experiment are shown in Fig. 20.1b. The location of maximum sensitivity to sound is slightly forward of the pan-bone area of the lower jaw, a location where Norris [20.5] hypothesized that sounds enter the head of a dolphin. Numerical simulation work by Aroyan [20.6] suggest that sounds enter the dolphin's head forward of the pan bone, but a good portion of the sound propagates below the skin to the pan bone and enters the head through the pan bone. The fact that sounds probably propagate through the lower jaw of dolphins and other

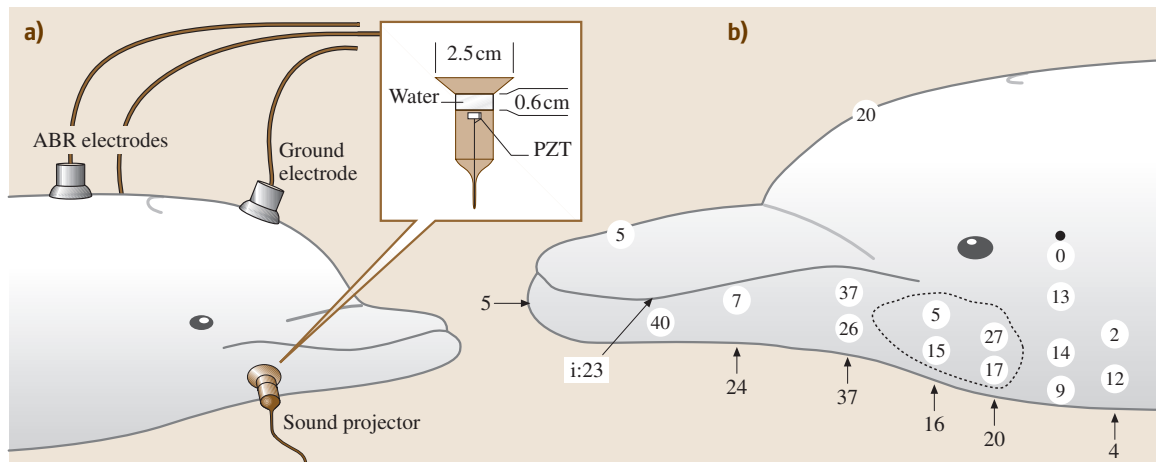


Fig. 20.1 (a) The experimental geometry used by Møhl et al. [20.2], (b) results of the auditory brainstem response (ABR) threshold measurements. The numerical values represent the amount of attenuation of the sound needed to obtain an ABR threshold. Therefore, the higher the number the more sensitive the location

odontocetes does not necessarily mean that the same or a similar propagation process is occurring with baleen whales.

20.1.1 Hearing Sensitivity of Odontocetes

Almost all our knowledge of hearing in cetaceans comes from studies performed with small odontocetes. The most studied species is the Atlantic bottlenose dolphin (*tursiops truncatus*). Despite the amount of research performed with the bottlenose dolphin, our understanding of auditory processes in these animals lags considerably behind that for humans and other terrestrial mammals. There are still many large gaps in our knowledge of various auditory processes occurring within the most studied odontocetes. The first audiogram for a cetacean was measured by Johnson [20.9] for a *tursiops truncatus*. Since then, audiograms have been determined for the harbor porpoise (*phocoena phocoena*) by Andersen [20.10] and Kastelein et al. [20.11], the killer whale (*orcinus orca*) by Hall and Johnson [20.12] and Szymanski et al. [20.13], the beluga whale (*delphinapterus leucas*) by White et al. [20.14], the Pacific bottlenose dolphin (*tursiops gilli*) by Ljungblad et al. [20.15], the false killer whale (*pseudorca crassidens*) by Thomas et al. [20.16], the Chinese river dolphin (*lipotes vexillifer*) by Wang et al. [20.17], Risso's dolphins (*grampus griseus*) by Nachtigall et al. [20.18], the tucuxi (*sotalia fluviatilis*) by Sauerland and Dehnhardt [20.19], and the striped dolphin (*stenella coeruleoalba*) by Kastelein

et al. [20.20]. The audiograms of these odontocetes are shown in Fig. 20.2. It is relatively striking to see how similar the audiograms are between species considering the vastly different habitats and areas of the world where some of these animals are found and the large differences in body size. All the audiograms suggest high-frequency hearing capabilities, with the smallest animal, *phocoena phocoena* having the highest hearing limit close to 180 kHz. However, the *orcinus orca*, which is over 95 times heavier and about six times longer can hear up to about 105 kHz. The actual threshold values shown in Fig. 20.2 should not be compared between species because the different methods of determining the threshold can lead to different results and because of the difficulties of obtaining good sound pressure level measurements in a reverberant environment. For example, Kastelein et al. [20.11] used a narrow-band frequency-modulated (FM) signal to avoid multi-path problems and the FM signals may provide additional cues not present in a pure-tone signal. Nevertheless, the audiograms shown in Fig. 20.2 suggest that all the animals had similar thresholds of 10–15 dB.

A summary of some important properties of the different audiograms depicted in Fig. 20.2 is given in Table 20.1. In the table, the frequency of best hearing is arbitrary defined as the frequency region in which the auditory sensitivity is within 10 dB of the maximum sensitivity depicted in each audiogram of Fig. 20.2. With the exception of the *Orcinus* and the *Lipotes*, the maximum sensitivity of the rest of the species represented

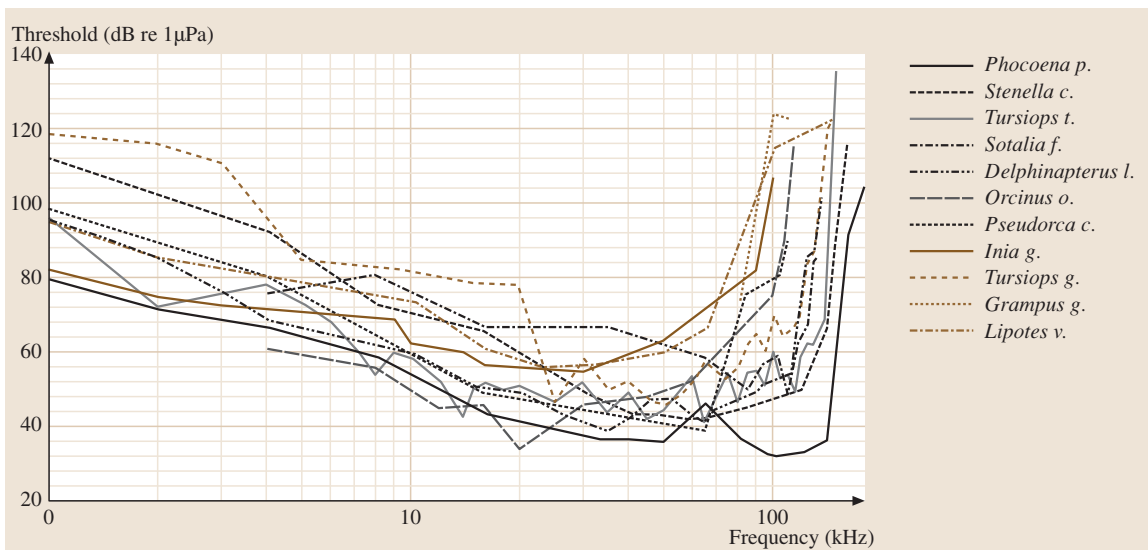


Fig. 20.2 Audiogram for different odontocetes species (after [20.7, 8])

Table 20.1 Some important properties of the audiograms plotted in Fig. 20.2

Species	Maximum sensitivity (dB re 1 : Pa)	Frequency of best hearing (kHz)	Upper frequency limit (kHz)
<i>phocoena phocoena</i>	32	18 – 130	180
<i>stenella coeruleoalba</i>	42	30 – 125	160
<i>tursiops truncatus</i>	42	15 – 110	150
<i>tursiops gilli</i>	47	30 – 80	135
<i>sotalia fluviatilis</i>	50	35 – 50	135
<i>delphinapterus leucas</i>	40	11 – 105	120
<i>pseudorca crassidens</i>	39	17 – 74	115
<i>orcinus orca</i>	34	15 – 40	110
<i>inia geoffrensis</i>	51	12 – 64	100
<i>lipotes vexillifer</i>	55	15 – 60	100
<i>grampus griseus</i>	–	–	100

in Fig. 20.2 and Table 20.1 are very similar, and within experimental uncertainties, especially for audiograms obtained with the staircase procedure using relatively large step sizes of 5 dB or greater. At the frequency of best hearing, the threshold for *Orcinus* and *Phocoena* are much lower than for the other animals. It is not clear whether this keen sensitivity is a reflection of a real difference or a result of some experimental artifact. The data of Table 20.1 also indicate that *Phocoena phocoena*, *Stenella coeruleoalba* and *Tursiops truncatus* seem to have the widest auditory bandwidth.

20.1.2 Directional Hearing in Dolphins

Sound Localization

The ability to localize or determine the position of a sound source is important in order to navigate, detect prey and avoid predators and avoid hazards producing an acoustic signatures. The capability to localize sounds has been studied extensively in humans and in many vertebrates (see [20.21]). Lord Rayleigh in 1907 proposed that humans localized in the horizontal plane by using interaural time differences for low-frequency sounds and interaural intensity differences for high-frequency sounds. The sound localization acuity of a subject is normally defined in terms of a minimum audible angle (MAA), defined as the angle subtended at the subject by two sound sources, one being at a reference azimuth, at which the subject can just discriminate the sound sources as two discrete sources [20.22]. If the sound sources are separated symmetrically about a midline, the MAA is one half the threshold angular separation between the sound sources. If one of the sound sources is located at the midline, then the MAA is the same as the threshold angular separation between the two sources.

Renaud and Popper [20.23] examined the sound localization capabilities of a *tursiops truncatus* by measuring the MAA in both the horizontal and vertical planes. During a test trial the dolphin was required to station on a bite plate facing two transducers positioned at equal angles from an imaginary line running through the center of the bite plate. An acoustic signal was then transmitted from one of the transducers and the dolphin was required to swim and touch the paddle on the same side as the emitting transducer. The angle between the transducers was varied in a modified staircase fashion. If the dolphin was correct for two consecutive trials, the transducers were moved an incremental distance closer together, decreasing the angle between the transducer by 0.5°. After each incorrect trial, the transducers were moved an incremental distance apart, increasing the angle between the transducers by 0.5°. This modified staircase procedure allowed threshold determination at the 70% level. The threshold angle was determined by averaging a minimum of 16 reversals. A randomized schedule for sound presentation through the right or left transducer was used.

The localization threshold determined in the horizontal and vertical planes as a function of frequency for narrow-band pure-tone signals is shown in Fig. 20.3. The MAA had a U-shaped pattern, with a large value of 3.6° at 6 kHz, decreasing to a minimum of 2.1° at 20 kHz and then slowly increasing in an irregular fashion to 3.8° at 100 kHz. MAAs for humans vary between 1° and 3.7°, with the minimum at a frequency of approximately 700 Hz [20.24]. The region where the MAA decreased to a minimum in Figs. 20.19 and 20.20 (about 20 kHz) may be close to the frequency at which the dolphin switches from using interaural time difference cues to interaural intensity difference cues. The MAAs for the

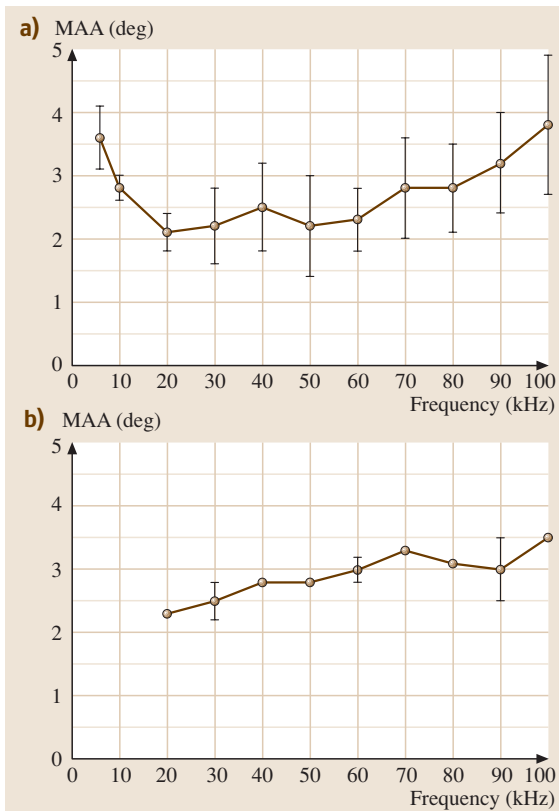


Fig. 20.3 (a) Localization threshold determined in the horizontal plane as a function of frequency. The mean \pm one standard deviation is shown for seven determinations per frequency. The animal faced directly ahead at 0° azimuth. (b) Localization threshold determined in the vertical plane as a function of frequency. Standard deviation are indicated for 30, 60 and 90 kHz vertical data (seven sessions each). The dolphin's azimuth was 0° (after *Renauld and Popper*, [20.27]) Figs. 20.19 and 20.20

bottlenose dolphin were smaller than the MAAs (in the horizontal plane) of 3.5° at 3.5 kHz and 6° at 6 kHz for a harbor porpoise measured by *Dudok van Heel* [20.25], and 3° at 2 kHz, measured by *Andersen* [20.26] also for a harbor porpoise.

In order to measure the MAA in the vertical plane, the dolphin was trained to turn to its side (rotate its body 90° along its longitudinal axis) and to bite on a sheet of plexiglass which was used as the stationing device. The MAA in the vertical plane varied between 2.3° at 20 kHz to 3.5° at 100 kHz. These results indicate that the animal could localize in the vertical plane nearly as well as in the horizontal plane. These results were

not expected since binaural affects, whether interaural time or intensity, should not be present in the vertical plane. However, the dolphin's ability to localize sounds in the vertical plane may be explained in part by the asymmetry in the receive beam patterns in the vertical plane discussed in the next section.

Renauld and Popper [20.23] also determined the MAA for a broadband transient signal or click signal, having a peak frequency of 64 kHz and presented to the dolphin at a repetition rate of 333 Hz. The MAA in the horizontal plane was found to be approximately 0.9° and 0.7° in the vertical plane. It is not surprising that a broadband signal should result in a lower MAA than a pure-tone signal of the same frequency as the peak frequency of the click. The short onset time and the broad frequency spectrum of a click signal should provide additional cues for localization.

Receiving Beam Patterns

Having narrow transmission and reception beams allows the dolphin to localize objects in a three-dimensional volume, spatially separate objects within a multi-object field, resolve features of extended or elongated objects, and to minimize the amount of interference received. The amount of ambient noise from an isotropic noise field and the amount of reverberation interference received is directly proportional to the width of the receiving beam. The effects of discrete or partially extended interfering noise or reverberant sources can be minimized by simply directing the beams away from the sources.

The receiving beam pattern of a dolphin was determined by measuring the masked hearing threshold as a function of the azimuth about the animal's head. The relative masked hearing threshold as a function of azimuth is equivalent to the received beam pattern since the receiving beam pattern is the spatial pattern of hearing sensitivity. *Au and Moore* [20.28] measured the dolphin's masked hearing threshold as the position of either the noise or signal sources varied in their angular position about the animal's head. The dolphin was required to voluntarily assume a stationary position on a bite plate constructed out of a polystyrene plastic material. The noise and signal transducers were positioned along an arc with the center of the arc located approximately at the pan bone of the animal's lower jaw. In order to measure the dolphin's receiving beam in the vertical plane, the animal was trained to turn onto its side before biting the specially designed vertical bite-plate stationing device. For the measurement in the vertical plane, the position of the signal transducer was fixed directly in

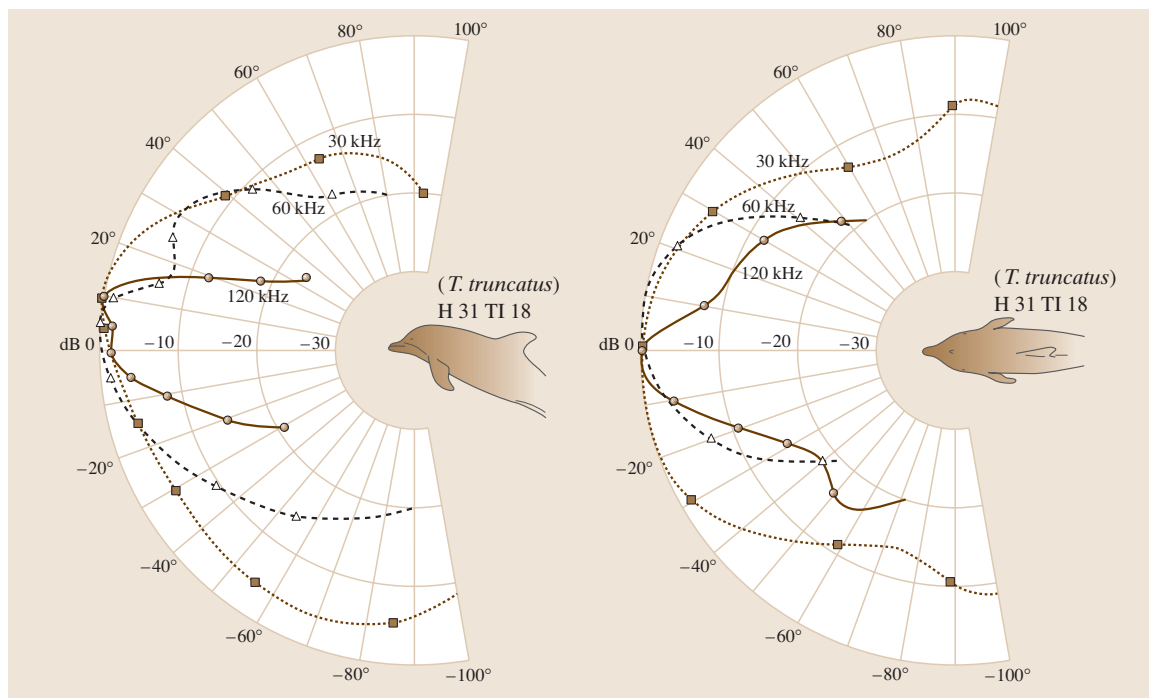


Fig. 20.4 Receive beam patterns in the vertical and horizontal planes for frequencies of 30, 60 and 120 kHz. The relative masked thresholds as a function of the elevation angle of the asking noise source are plotted for each signal frequency (after Au and Moore, [20.28])

line with the bite plate and its acoustic output was held constant. Masked thresholds were measured for different angular position of the noise transducer along the arc. The level of the noise was varied in order to obtain the masked threshold. A threshold estimate was considered complete when at least 20 reversals (10 per session) at a test angle had been obtained over at least two consecutive sessions, and if the average reversal values of the two sessions were within 3 dB. After a threshold estimate was achieved, the noise transducer was moved to a new azimuth over a set of randomly predesignated azimuths. As the azimuth about the dolphin's head increased, the hearing sensitivity of the dolphin tended to decrease, requiring higher levels of masking noise from a transducer located at that azimuth to mask the signal from a source located directly ahead of the animal.

The receiving beam patterns in both the vertical and horizontal plane are plotted for signal frequencies of 30, 60 and 120 kHz in Fig. 20.4. The radial axis of Fig. 20.4 represents the difference in dB between the noise level needed to mask the test signal at any azimuth and the minimum noise level needed to mask the test signal at the azimuth corresponding to the major axis of the

vertical beam. The shape of the beams in Fig. 20.4 indicates that the patterns were dependent on frequency, becoming narrower, or more directional as the frequency increased. The beam of a planar hydrophone also becomes narrower as frequency increases. The 3 dB beam widths were approximately 30.4°, 22.7°, and 17.0° for frequencies of 30, 60, and 120 kHz, respectively. There was also an asymmetry between the portion of the beam above and below the dolphin's head. The shape of the beams dropped off more rapidly as the angle above the animal's head increased than for angles below the animal's head, indicating a more rapid decrease in the animal's hearing sensitivity for angles above the head than for angles below the head. If the dolphin receives sounds through the lower jaw, the more rapid reduction in hearing sensitivity for angles above the head may have been caused by shadowing of the received sound by the upper portion of the head structure including air in the nasal sacs [20.29]. There is a slight peculiarity in the 60 kHz beam which shows almost the same masked threshold values for 15° and 25° elevation angles.

The radial line passing through the angle of maximum sensitivity is commonly referred to as the major

axis of the beam. The major axis of the vertical beams is elevated between 5° and 10° above the reference axis. The 30 and 120 kHz results show the major axis at 10° while the 60 kHz results showed the major axis at 5° . It will be shown in a later section that the major axis of the received beam in the vertical plane is elevated at approximately the same angle as the major axis of the transmitted beam in the vertical plane.

In the horizontal beam pattern measurement, two noise sources were fixed at azimuth angles of $\pm 20^\circ$. The level of the noise sources was also fixed. The position of the signal transducer was varied from session to session. Masked thresholds were determined as a function of the azimuth of the signal transducer, by varying the signal level of the signal transducer in a staircase fashion. A threshold estimate was considered completed when at least 20 reversals at a test angle had been obtained over at least two consecutive sessions, if the average reversal values were within 3 dB of each other. After a threshold estimate was determined, the signal transducer was moved to a new azimuth over a set of randomly predesignated azimuths. Two noise sources were used in order to discourage the dolphin from internally steering its beam in the horizontal plane. If the animal could steer its beam, it would receive more noise from one of the two hydrophones, and therefore not experience any improvement in the signal-to-noise ratio. The masking noise from the two sources was uncorrelated but equal in amplitude. The radial axis represents the difference in dB between the signal level at the masked threshold for the various azimuths and the signal level of the masked threshold for 0° azimuth (along the major axis of the horizontal beam). The horizontal receiving beams were directed forward with the major axis being parallel to the longitudinal axis of the dolphin. The beams were nearly symmetrical about the major axis. Any asymmetry was within the margin of experimental error involved in estimating the relative thresholds. The horizontal beam patterns exhibited a similar frequency dependence as the vertical beam patterns, becoming narrower or more directional as the frequency increased. The 3 dB beam widths were 59.1° , 32.0° , and 13.7° for frequencies of 30, 60, and 120 kHz, respectively.

Zaytseva et al. [20.30] measured the horizontal beam pattern of a dolphin by measuring the masked hearing threshold as a function of azimuth. Their beam width of 8.2° for a frequency of 80 kHz was much narrower than the 13.7° for a frequency of 120 kHz. The difference in beam width is even larger if the results of Au and Moore [20.28] are linearly interpolated to 80 kHz.

We calculated an interpolated beam width of 25.9° at 80 kHz, which was considerably greater than the 8.2° obtained by Zaytseva et al. [20.30]. The difference in beam width measured by Zaytseva et al. and Au and Moore may be attributed to the use of only one noise source by Zaytseva et al. compared to the two noise sources used by Au and Moore. With a single masking noise source in the horizontal plane, there is the possibility of the animal performing a spatial filtering operation by internally steering the axis of its beam in order to maximize the signal-to-noise ratio. Another possibility is that Zaytseva et al. did not use a fixed stationing device. Rather, the dolphin approached the signal hydrophone from a start line, always oriented in the direction of the signal hydrophone. The animal responded to the presence or absence of a signal by either swimming or not swimming to the hydrophone. In such a procedure, it is impossible to control the orientation of the animal's head with respect to the noise masker so that the dolphin could move its head to minimize the effects of the noise.

Directivity Index

The directivity index is a measure of the sharpness of the beam or major lobe of either a receiving or transmitting beam pattern. For a spherical coordinate system, the directivity index of a transducer is given by the equation [20.31]

$$DI = 10 \log \frac{4\pi}{\int_0^{2\pi} \int_{-\pi/2}^{\pi/2} \left(\frac{p(\theta, \phi)}{p_0} \right)^2 \sin \theta \, d\theta \, d\phi} . \quad (20.1)$$

Although the expression for directivity index is relatively simple, using it to obtain numerical values can be quite involved unless transducers of relatively simple shapes (cylinders, lines and circular apertures) with symmetry about one axis is involved. Otherwise, the beam pattern needs to be measured as a function of both θ , and ϕ . This can be done by choosing various discrete values of θ and measuring the beam pattern as a function of ϕ , a tedious process. Equation (20.1) can then be evaluated by numerically evaluating the double integral with a digital computer. The directivity indices associated with the dolphin's beam patterns in Fig. 20.4 were estimated by Au and Moore [20.28] using (20.1) and a two-dimensional Simpson's 1/3-rule algorithm [20.32]. The results of the numerical evaluation of are plotted as a function of frequency in Fig. 20.5. DIs of 10.4, 15.3 and 20.6 dB were obtained for frequencies of 30, 60,

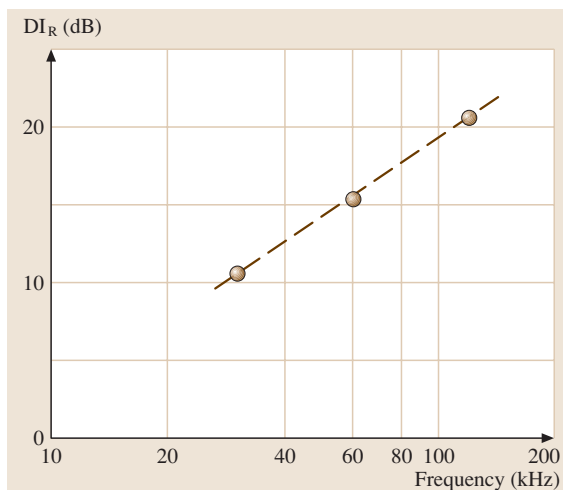


Fig. 20.5 Receiving directivity index as function of frequency for a *tursiops truncatus*

and 120 kHz, respectively. A linear curve fitted to the computed DIs in a least-square-error manner is also shown in the Fig. 20.5. The equation of the line is

$$\text{DI}(\text{dB}) = 16.9 \log f(\text{kHz}) - 14.5. \quad (20.2)$$

The results of Fig. 20.5 indicate that the dolphin's receive directivity index increased with frequency in a manner similar to that of a linear transducer (Bobber, 1970). The expression in (20.2) is only valid for frequencies at which DI(dB) is greater or equal to 0.

Although the directivity index expressed by (20.1) is for a *tursiops*, it can also be used to estimate the directivity index of other dolphins by applying an appropriate correction factor, so that (20.2) can be rewritten as

$$\text{DI}(\text{dB}) = 16.9 \log f(\text{kHz}) - 14.5 + \text{CF}(\text{dB}), \quad (20.3)$$

where CF(dB) is a correction factor taking into account different head sizes. The directivity index of a planar circular plate is proportional to its diameter so if we let d_T be the diameter of the head of a *tursiops* at about the location of the blowhole and d_D be the diameter of the head of a different species of dolphin, then the correction factor can be expressed as

$$\text{CF}(\text{dB}) = 20 \log(d_D/d_T). \quad (20.4)$$

The correction factor will be positive for a dolphin with a larger head and negative for a dolphin with a smaller head than *tursiops*.

20.1.3 Hearing by Mysticetes

Our knowledge of the hearing characteristics of baleen whales is extremely limited. We do not know how they receive sounds, the frequency range of hearing, and the sensitivity of hearing at any frequency. Much of our understanding of hearing in baleen whales comes from anatomical studies of the ears of different species. Baleen whales have occluded external auditory canals that are filled with a homogeneous wax [20.33]. The lower jaws of mysticetes are designed for sieving or gulp feeding and have no evident connection to the temporal bones [20.33] making it very difficult to understand how sounds enter into the ears of these whales.

Various types of whales have been observed by many investigators to react strongly and drastically change their behavior in the presence of boats and low-flying aircraft, however, the sound pressure levels at the whales' locations are often difficult to define and measure. In some situations, the sound levels of the aversive sound could be estimated and a data point obtained. Bowhead whales were observed fleeing from a 13 m diesel-powered boat having a noise level at the location of the whales of about 84 dB re $1 \mu\text{Pa}$ in the dominant 1/3-octave band, or about 6 dB above the ambient noise in that band [20.34]. Playback experiments with bowhead whales indicated that they took evasive action when the noise was about 110 dB re $1 \mu\text{Pa}$ or 30 dB above the ambient noise in the same 1/3-octave band [20.35]. Playback experiments with migrating gray whales indicated that about 10% of the whales made avoidance behavior when the noise was about 110 dB in a 1/3 octave band, 50% at about 117 dB and 90% at about 122 dB or greater. These playback signals consisted of anthropogenic noise associated with the oil and gas industry.

Frankel [20.36] played back natural humpback whale sounds and a synthetic sound to humpback whales wintering in the waters of the Hawaiian islands. Twenty seven of the 1433 trials produced rapid approach response. Most of the responses were to the feeding call. Feeding call and social sounds produced changes in both separation and whale speed, indicating that these sounds can alter a whale's behavior. The humpback whales responded to sounds as low as 102–105 dB but the strongest responses occurred when the sounds were 111 to 114 dB re $1 \mu\text{Pa}$.

All of the playback experiments suggest that sounds must be between 85 and 120 dB before whales will react to them. These levels are very high compared to those that dolphins can hear and may suggest that it is very

difficult to relate reaction to hearing sensitivity. Whales may not be reacting strongly unless the sounds are much higher than their hearing threshold.

Determining the hearing sensitivity or audiogram of baleen whales represents an extremely difficult challenge and will probably require the use of some sort of electrophysiological technique as suggested by *Ridgway et al.* [20.37]. Perhaps a technique measuring auditory-evoked potentials with beached whales may provide a way to estimate hearing sensitivity. Even with evoked potential measurements, there are many issues that have to be considered. For example, if an airborne source is used, the results cannot be translated directly to the underwater situation. If a sound source is placed

on a whale's head, relating that to a whale receiving a plane wave will also not be simple. Measurement of evoked potentials themselves may not be simple because of the amount of flesh, muscles and blubber that the brain waves would have to travel through in order to reach the measurement electrodes. *Ridgway and Carder* [20.38] reported on some attempts to use the evoked potential method with a young gray whale held at Sea World in California. They also showed that the pygmy whale auditory system was most sensitive to very high frequencies (120–130 kHz) in the same range as their narrow-band echolocation pulses. A young sperm whale was most sensitive in the 10–20 kHz region of the spectrum [20.38].

20.2 Echolocation Signals

Echolocation is the process in which an organism projects acoustic signals and obtains a sense of its surroundings from the echoes it receives. In a general sense, any animal with a capability to hear sounds can echolocate by emitting sounds and listening to the echoes. A person in an empty room can gain an idea of the size and shape of the room by emitting sounds and listening to the echoes from the different walls. However, in this chapter, echolocation is used in a more specific sense in which an animal has a very specialized capability to determine the presence of objects considerably smaller than itself, discriminate between various objects, recognize specific objects and localize objects in three-dimensional space (determine range and azimuth). Dolphins and bats have this specialized capability of echolocation.

The echolocation system of a dolphin can be broken down into three subsystems: the transmission, reception and signal processing/decision subsystems. The reception system has to do with hearing and localization. The transmission system consist of the sound production mechanism, acoustic propagation from within the head of the dolphin to into the water, and the characteristics of the signals traveling in the surrounding environment. The third subsystem has to do with processing of auditory information by the peripheral and central nervous system. The capability of a dolphin to detect objects in noise and in clutter, and to discriminate between various objects depends to a large extent on the information-carrying capabilities of the emitted signals.

Dolphins most likely produce sounds within their nasal system and the signals are projected out through the melon. Although there has been a long-standing controversy on whether sounds are produced in the larynx or in the nasal system of odontocetes, almost all experimental data with dolphins indicate that sounds are produced in the nasal system [20.39]. For example, *Ridgway and Carder* [20.40] used catheters accepted into the nasal cavity by trained belugas. The belugas performed an echolocation task in open water, detecting targets and reported the presence of targets by whistling. Air pressure within the nasal cavity was shown to be essential for echolocation and for whistling [20.40].

The melon immediately in front of the nasal plug may play a role in channeling sounds into the water, a notion first introduced by *Wood* [20.41]. *Norris and Harvey* [20.42] found a low-velocity core extending from just below the anterior surface towards the right nasal plug, and a graded outer shell of high-velocity tissue. Such a velocity gradient could channel signals originating in the nasal region in both the vertical and horizontal planes. Using both a two-dimensional [20.43] and a three-dimensional model [20.6] to study sound propagation in a dolphin's head, Aroyan has shown that echolocation signals most likely are generated in the nasal system and are channeled into the water by the melon. *Cranford* [20.44] has also collected evidence from nasal endoscopy of trained echolocating dolphins that suggest that echolocation signals are most likely produced in the nasal system at the location of the monkey-lips, dorsal bursae complex just beneath the blow hole.

20.2.1 Echolocation Signals of Dolphins that also Whistle

Most dolphin species are able to produce whistle signals. Among some of the species in this category in which echolocation signals have been measured include the bottlenose dolphin (*tursiops sp.*), beluga whale (*delphinapterus leucas*), killer whale (*orcinus orca*), false killer whale (*pseudorca crassidens*), Pacific white-sided dolphin (*lagenorhynchus obliquidens*), Amazon river dolphin (*inia geoffrensis*), Risso's dolphin (*grampus griseus*), tucuxi (*sotalia fluviatilis*), Atlantic spotted dolphin (*stenella frontalis*), Pacific spotted dolphin (*Stenella attenuata*), spinner dolphin (*Stenella longirostris*), pilot whale (*globicephala sp.*), rough-toothed dolphin (*steno bredanensis*), Chinese river dolphin (*lipotes vexillifer*) and sperm whales (*physeter catodon*). However, most of the available data have been obtained for three species: the bottlenose dolphin, the beluga whale and the false killer whale.

Prior to 1973, most echolocation signals of *tursiops* were measured in relatively small tanks and the results provided a completely different picture of what

we currently understand. It was not until the study of Au et al. [20.45] that certain features of biosonar signals used by *tursiops* and other dolphins in open waters were discovered. We discovered that the signals had peak frequencies between 120 and 130 kHz, over an octave higher than previously reported peak frequencies between 30 and 60 kHz [20.46]. We also measured an average peak-to-peak click source level on the order of 220 dB re 1 μ Pa at 1 m, which represents a level 30 to 50 dB higher than previously measured for *tursiops*. Examples of typical echolocation signals emitted by *tursiops truncatus* are shown in Fig. 20.6 for two situations. The top signal is typical of signals used in the open waters of Kaneohe Bay, Oahu, Hawaii, and the second signal represents typical signals for a *tursiops* in a tank. Signals measured in Kaneohe Bay regularly have duration between 40 and 70 μ s, 4 to 10 positive excursion, peak frequencies between 110 and 130 kHz and peak-to-peak source levels between 210 and 228 dB re 1 μ Pa. The signals in Fig. 20.6 are not drawn to scale; if they were, the tank signal would resemble a flat line.

Au et al. [20.47] postulated that high-frequency echolocation signals were a byproduct of the animals producing high-intensity clicks to overcome snapping shrimp noise. In other words, dolphins can only emit high-level clicks (greater than 210 dB) if they use high frequencies. The effects of a noisy environment on the echolocation signals used by a beluga or white whale (*Delphinapterus leucas*) was vividly demonstrated by Au et al. [20.47]. The echolocation signal of a beluga was measured in San Diego Bay, California before the whale was moved to Kaneohe Bay. The ambient noise in Kaneohe Bay is between 15 to 20 dB greater than in San Diego Bay. The whale emitted echolocation signals with peak frequencies between 40 and 60 kHz and with a maximum averaged peak-to-peak source level of 202 dB re 1 μ Pa in San Diego Bay. In Kaneohe Bay, the whale shifted the peak frequency of its signals over an octave higher to 100 and 120 kHz. The source level also increased to over 210 dB re 1 μ Pa [20.47]. Examples of typical echolocation signals used by the whale in San Diego and in Kaneohe Bay are shown in Fig. 20.7a. Here, the signals are drawn to scale with respect to each other. Echolocation signals used by belugas in tanks also resemble the low-frequency signals shown in Fig. 20.2a [20.48, 49]. Turl et al. [20.50] measured the sonar signals of a beluga in a target-in-clutter detection task in San Diego Bay and found the animal used high-frequency (peak frequency above 100 kHz) and high-intensity (greater than 210 dB re 1 μ Pa) signals. Therefore low-amplitude clicks of the beluga had

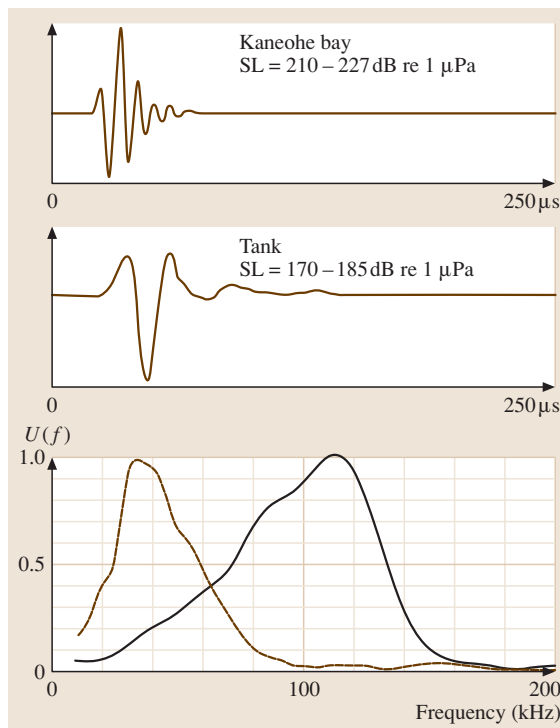


Fig. 20.6 Example of echolocation signals used by *tursiops truncatus* in Kaneohe Bay (after Au [20.45]), and in a tank

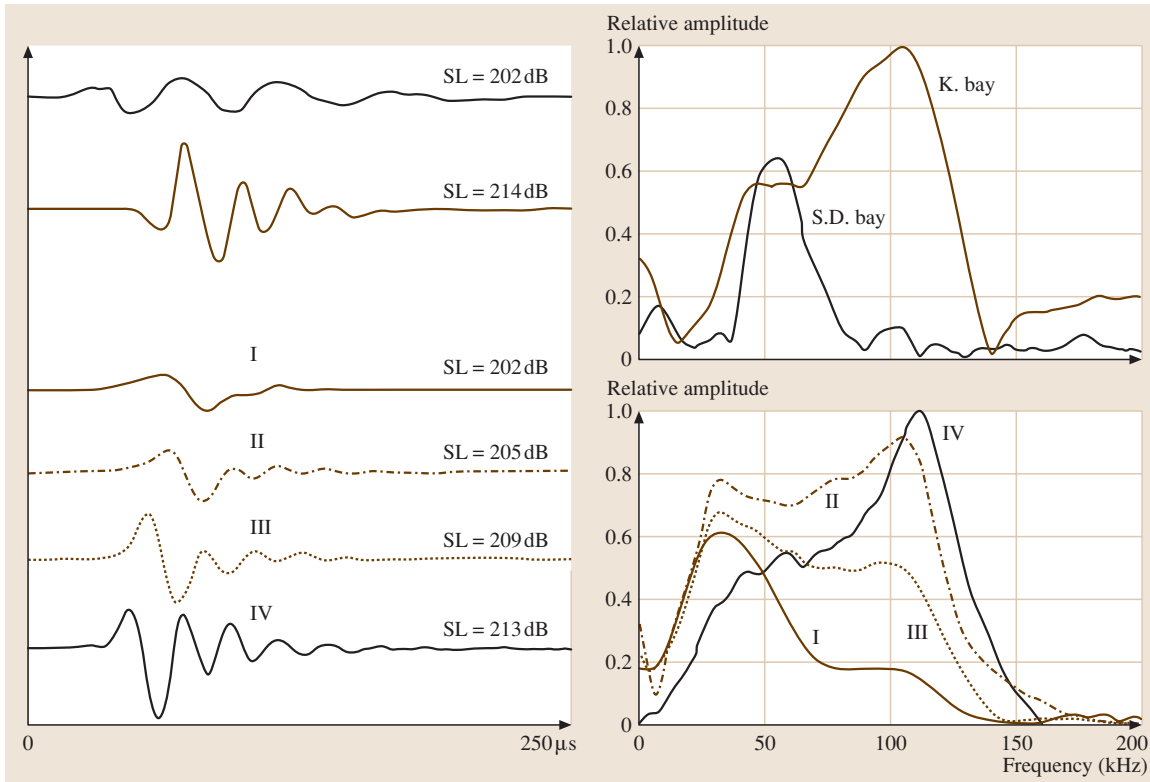


Fig. 20.7 (a) Example of beluga echolocation signals measured in San Diego Bay and in Kaneohe Bay (after Au et al. [20.47]); (b) Examples of *pseudorca* echolocation signals, SI is the averaged peak-to-peak source level (after Au et al. [20.52])

low peak frequencies and the high-amplitude clicks had high peak frequencies. The data of Moore and Pawloski [20.51] for *Tursiops* also seem to support the notion that the shape of the signal in the frequency domain is related to the intensity of the signal.

Recent results with a false killer whale showed a clear relationship between the frequency content of echolocation signals and source level [20.52]. The *Pseudorca* emitted four basic types of signals, which are shown in Fig. 20.7b. The four signal types have spectra that are bimodal (having two peaks); the spectra in Fig. 20.2 are also bimodal. The type I signals were defined as those with the low-frequency peak (< 70 kHz) being the primary peak and the high-frequency peak being the secondary peak with its amplitude at least 3 dB below that of the primary peak. Type II signals were defined as those with a low-frequency primary peak and a high-frequency secondary peak having an amplitude within 3 dB of the primary peak. Type III signals were those with a high-frequency primary peak (>70 kHz),

and a low-frequency secondary peak having an amplitude within 3 dB of the primary peak. Finally, type IV signals were those with a high-frequency primary peak having an amplitude that was at least 3 dB higher than that of the secondary low-frequency peak.

The data of Thomas et al. [20.53, 54] also indicated a similar relationship between intensity and the spectrum of the signal. The echolocation signals of a *pseudorca* measured in a tank had peak frequencies between 20 and 60 kHz and source levels of approximately 180 dB re 1 μPa [20.53]. Most of the sonar signals used by another *pseudorca* performing a detection task in the open waters of Kaneohe Bay had peak frequencies between 100 and 110 kHz and source levels between 220 and 225 dB re 1 μPa [20.54].

A bimodal spectrum is best described by its center frequency, which is defined as the centroid of the spectrum, and is the frequency which divides the spectrum into two parts of equal energy. From Fig. 20.7, we can see that, as the source level of the signal in-

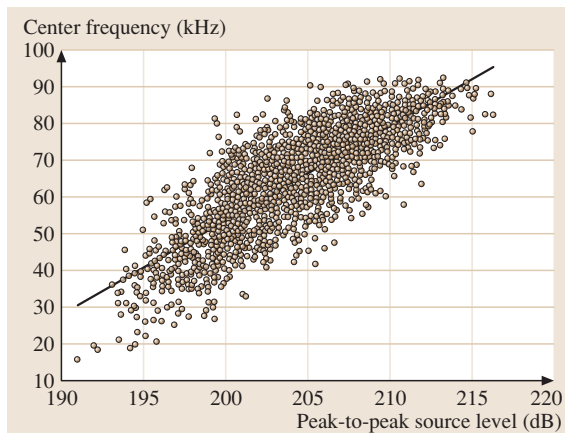


Fig. 20.8 Center frequency of echolocation signals emitted by a *pseudorca* as a function of the peak-to-peak source level (after Au et al. [20.52])

creased, the frequency components at higher frequencies also increased in amplitude, suggesting a relationship between source level and center frequency. This relationship can be examined by considering the scatter diagram of Fig. 20.8 showing center frequency plotted against source level. The solid line in the figure is a linear-regression curve fit of the data and has a correlation coefficient of 0.80.

The bimodal property of the echolocation signals of Fig. 20.7 seems to suggest that the response of the sound generator may be determined by the intensity of the driving force that eventually causes an echolocation signal to be produced. When the intensity of the driving force is low, only signals with low amplitudes and low-frequency peak are produced. Therefore, in small tanks, the signals resemble the tank signal of Fig. 20.1, and the bimodal feature is suppressed since the high-frequency portion of the source cannot be used for a low driving force. As the driving force increases to a moderate level, the low-frequency peak also increases in amplitude, and the high-frequency portion of the signal begins to come into use. As the driving force increases further the amplitude of the high-frequency peak becomes larger than that of the low-frequency peak, resulting in type III signals. As the driving force continues to increase to a high level, the amplitude of the high-frequency peak becomes much greater than the amplitude of the low-frequency peak and completely dominates the low-frequency peak causing the bimodal feature to be suppressed. Recent field measurements of free-ranging dolphins [20.55–57] suggest that the majority of echolocation clicks emitted by dolphins are bimodal.

The largest odontocete species is the sperm whale (*Physeter catodon*) and it too emits echolocation signals. Prior to the late 1990s the most prevalent understanding of sperm whale signals is that the clicks were broadband with peak frequencies between 4 and 8 kHz [20.58–61]. There were only two reports on source levels. Dunn [20.62] using sonobouys measured 148 sperm whale clicks from a solitary sperm whale and estimated an average peak-to-peak source level of 183 dB re 1 μ Pa. Levenson [20.59] estimated peak-to-peak source level of 180 dB re 1 μ Pa. The clicks were also thought to be essentially nondirectional and projected in codas [20.63]. Therefore, the notion of sperm whales echolocating was somewhat questionable. Part of the problem was the lack of measurements of sperm whale signaling in conjunction with foraging and the fact that click signals can have more than one function, such as communications and echolocation. In a review paper Watkins [20.63] spelled out his rationale for not supporting the notion of a sonar function for sperm whale clicks, “Other features of their sounds however, do not so easily fit echolocation:” Watkin’s rationale included his observations that clicks do not appear to be very directional, the inter-click interval does not varied as if a prey or obstacle is being approached, solitary sperm whales are silent for long periods, the level of their clicks appears to be generally greater than that required for echolocating prey or obstacles and the individual clicks are usually too long for good range resolution. It is important to state that most of Watkins measurements were conducted at low-temperate latitudes where females and calves are found.

Sperm whale echolocation began to be more fully understood with data obtained in ground-breaking work by Bertel Møhl and his students from the University of Aarhus, along with other Danish colleagues. They began to perform large-array aperture measurements of large bull sperm whales foraging along the slope of the continental shelf off Andenes, Norway beginning in the summer of 1977 [20.64]. Up to seven multi-platforms spaced on the order of 1 km apart were used in their study with hydrophones placed at depths varying from 5 to 327 m [20.65]. They also came up with a unique but logistically simple scheme of obtaining global positioning system (GPS) information to localize the position of each platform. Each platform continuously logged its position and time stamps on one track of a digital audio tape (DAT) recorder, the other track being used for measuring sperm whale clicks [20.64]. The GPS signals were converted to an analog signal by frequency-shift keying (FSK) modulation. In this way, each platform can be operated essentially autonomously and yet its lo-

cation and time stamps could be related to all the other platforms.

An important finding of *Møhl* et al. [20.64] is the monopulsed nature of on-axis clicks emitted by the sperm whales that were similar in shape and spectrum to dolphin echolocation signals but with peak frequencies between 15 and 25 kHz (this peak frequency range is consistent with the auditory sensitivity observed from evoked potential responses by a young sperm whale to clicks presented by *Ridgway* and *Carder* [20.38]). *Møhl* et al. [20.64] also estimated very high source levels as high as 223 dB re 1 μ Pa per RMS (root mean square). The per RMS measure is the level of a continuous sine wave having the same peak-to-peak amplitude as the click. This measure is clearly an overestimate of the RMS value of a sperm whale click. Nevertheless, the 223 dB reported by *Møhl* et al. [20.64] can easily be given a peak-to-peak value of 232 dB (adding 9 dB to the per-RMS value). In a follow-on study, *Møhl* et al. [20.65] measured clicks with RMS source levels as high as 236 dB re 1 μ Pa using the expression

$$p_{\text{RMS}} = \sqrt{\frac{1}{T} \int_0^T p^2(t) dt} . \quad (20.5)$$

For this measurement, they used a time interval corresponding to the 3 dB down points of the signal waveform. For this waveform, an RMS source level of 236 dB corresponds to a peak-to-peak source level of 243 dB re 1 μ Pa. Finally, they found that the clicks were very directional, as directional as dolphin clicks.

20.2.2 Echolocation Signals of Smaller Odontocetes that Do not Whistle

The second class of echolocation signals are produced by dolphins and porpoises that do not emit whistle signals. Not many odontocetes fall into this category and these non-whistling animals tend to be smaller than their whistling cousins. Included in this group of non-whistling odontocetes are the harbor porpoise (*phocoena phocoena*), finless porpoise (*neophocaena phocaenoides*), Dall's porpoise (*phocoenoides dalli*), Commerson's dolphin (*cephalorhynchus commersonii*), Hector's dolphin (*cephalorhynchus hectori*) and pygmy sperm whale (*kogia sp.*).

Examples of harbor porpoise and Atlantic bottlenose dolphin echolocation signals presented in a manner for easy comparison are shown in Fig. 20.9. There are four fundamental differences in the two types of echoloca-

tion signals. The non-whistling animal emit a signal with longer duration, narrower band, lower amplitude and single mode. The length of the *Phocoena phocoena* signal vary from about 125–150 μ s compared to 50–70 μ s for the *tursiops truncatus* signal. The bandwidth of the *Phocoena* signal is almost 0.2–0.3 that of the *tursiops* signal. Since the non-whistling dolphins are usually much smaller in length and weight than the whistling dolphins, the smaller animals might be amplitude limited in terms of their echolocation signals and compensate by emitting longer signals to increase the energy output. This issue can be exemplified by characterizing an echolocation click as [20.39]

$$p(t) = A s(t) , \quad (20.6)$$

where $A = |p|_{\text{max}}$ is the absolute value of the peak amplitude of the signal and $s(t)$ is the normalized wave-

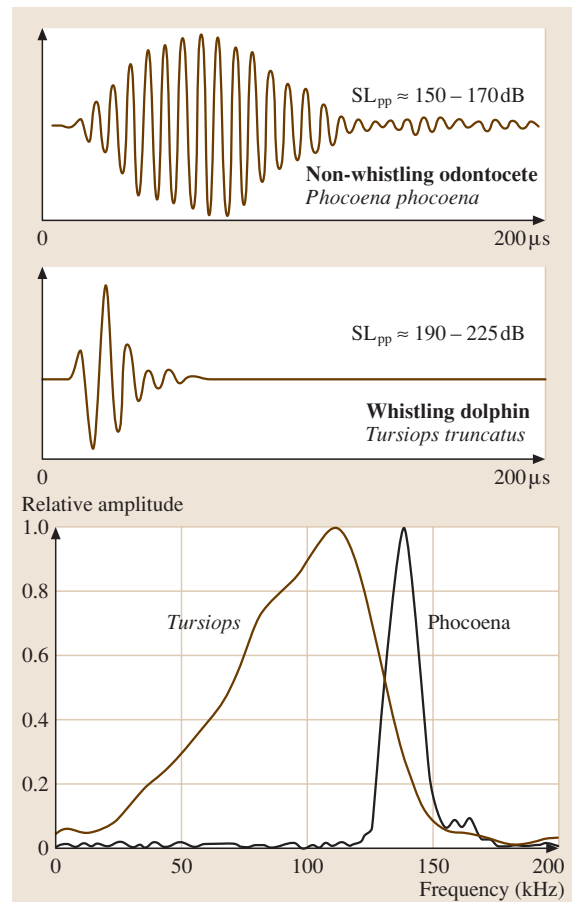


Fig. 20.9 Examples of typical echolocation signals of *phocoena phocoena* and *tursiops truncatus* (after [20.8])

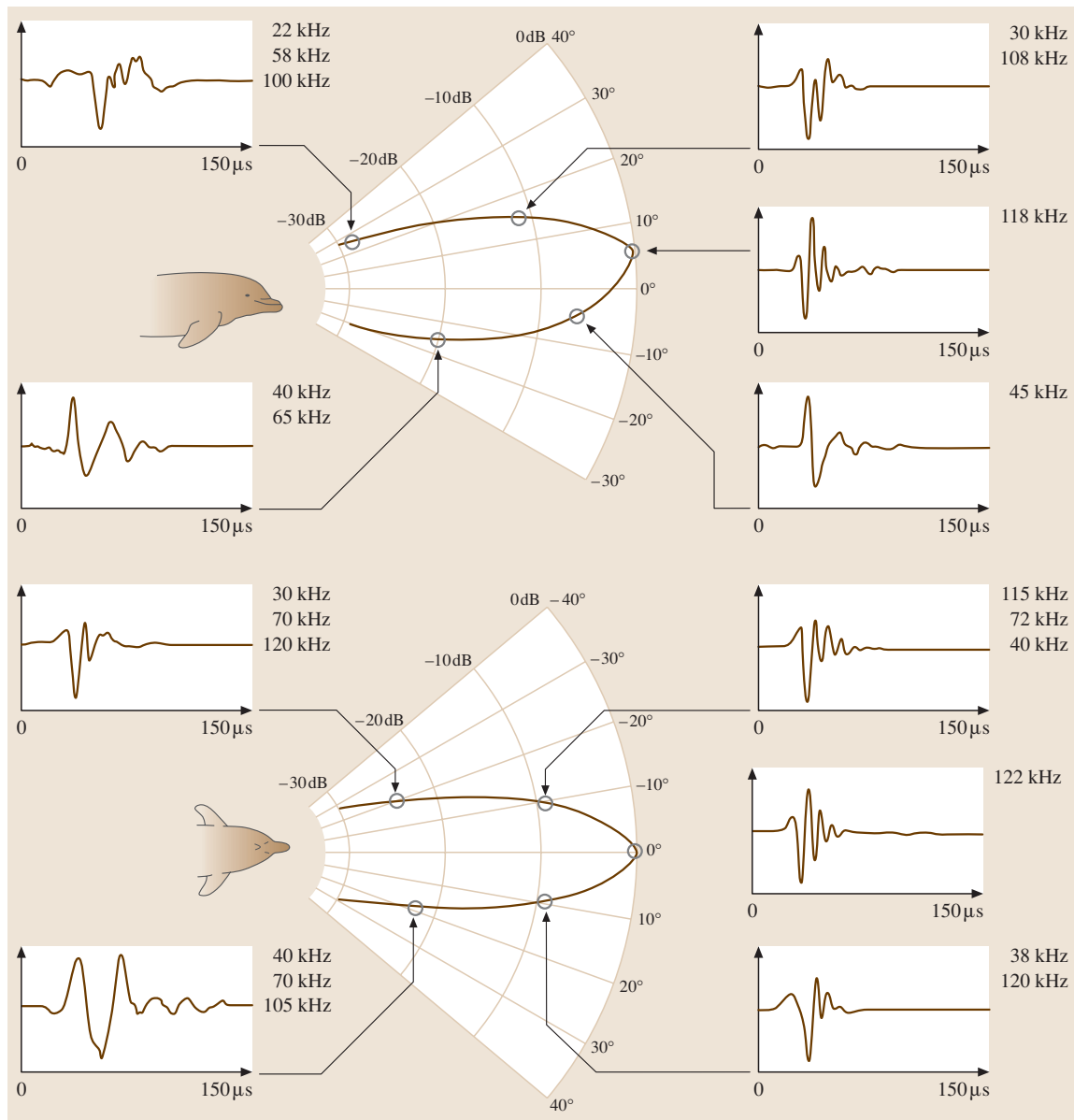


Fig. 20.10 The transmission beam pattern of a *tursiops truncatus* planes with the waveform of a click measured by 5–7 hydrophones (after Au [20.39]) in the vertical and horizontal planes

form having a maximum amplitude of unity. The source energy-flux density of the signal in dB can be expressed as

$$= 10 \log(A) + 10 \log \left(\int_0^T s(t)^2 dt \right), \quad (20.7)$$

$$SE = 10 \log \left(\int_0^T p(t)^2 dt \right)$$

where T is the duration of the signal. Letting $2A \approx$ be the peak-to-peak sound pressure level, (20.4) can be

rewritten as

$$SE = SL - 6 + 10 \log \left(\int_0^T s(t)^2 dt \right), \quad (20.8)$$

where SL is the the peak-to-peak source level and is approximately equal to $10 \log(2A)$. From Fig. 20.9, the *Tursiops* can emit signals with peak-to-peak source levels in open water that are greater than 50 dB for *phocoena*. The portion of the source energy that can be attributed to the length of the signal is only about 2–4 dB greater for *phocoena* than *Tursiops* [20.39]. Therefore, one can conclude that the target detection range of *phocoena* is considerably shorter than for *Tursiops*. This has been demonstrated by *Kastelein* et al. [20.67] who measured a target detection threshold range of 26 m for a 7.62 cm water-filled sphere in a quiet environment. The target detection range in a noisy environment and a similar 7.62 cm water-filled sphere was 113 m [20.68].

The echolocation signals of other non-whistling odontocetes are very similar to the *Phocoena phocoena* signal shown in Fig. 20.9. Examples of the echolocation signals of other non-whistling odontocetes can be found in *Au* [20.7, 39, 69]. Unfortunately, reliable source-level data have been collected only for *Phocoena phocoena* [20.70] and *Kogia* [20.69].

20.2.3 Transmission Beam Pattern

The outgoing echolocation signals of dolphins and other odontocetes are projected in a directional beam that have been measured in the vertical and horizontal planes for the bottlenose dolphin [20.39], beluga whale [20.66] and the false killer whale [20.52]. The composite beam pattern from the three measurements on *Tursiops* along with the averaged waveform from a single trial measured by 5 or the 7 hydrophones are shown in Fig. 20.10. The 3 dB beam width for the bottlenose dolphin was approximately 10.2° in the vertical plane and 9.7° in the horizontal plane. The waveforms detected by the various hydrophones in Fig. 20.10 indicate that signals measured away from the beam axis will be distorted with respect to the signals measured on the beam axis. The further away from the beam axis the more distorted the signals will be. This distortion come from the broadband nature of the click signals emitted by whistling dolphins. This characteristics also make it difficult to get good measurements of echolocation signals in the field even with an array of hydrophones since it is extremely difficult to obtain on-axis echolocation signals and also to know the orientation of the animal with respect to the measuring hydrophones. The frequencies shown with each waveform are the fre-

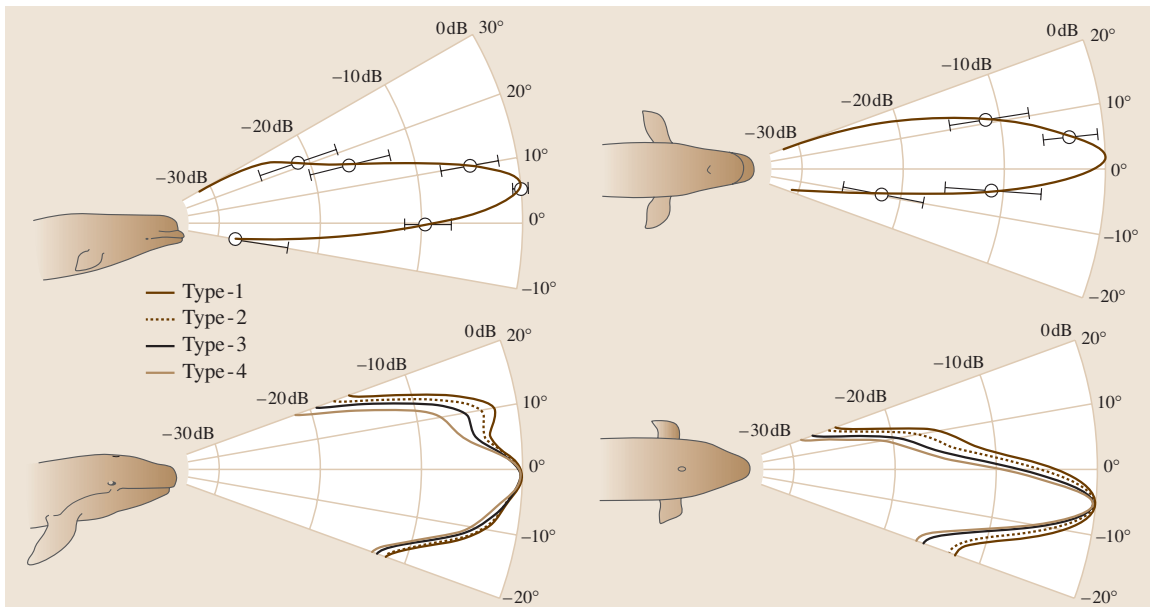


Fig. 20.11 The transmission beam pattern of a *delphinapterus leucas* (after *Au* et al. [20.66]) and a *pseudorca crassidens* (after *Au* et al. [20.52]) in the vertical and horizontal planes

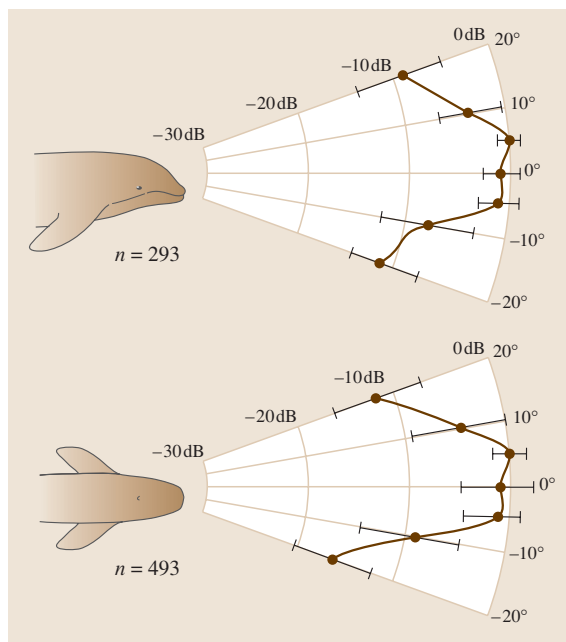


Fig. 20.12 Beam patterns in the vertical and horizontal planes for *phocoena phocoena* (Au et al. [20.70])

quencies of local maxima in the spectrum. At some angles the averaged signal had multiple peaks in the spectrum and these peaks are listed in order of prominence.

The beam patterns for the beluga and false killer whale are shown in Fig. 20.11. The beam width for the beluga whale was approximately 6.5° in both planes. Four beam patterns corresponding to the four signal types described in Fig. 20.7 are shown for the false killer whale. For the highest frequency (type IV signal) the 3 dB beam width in the vertical plane was approximately 10° , and 7° in the horizontal plane. The beam axis in the vertical plane for the bottlenose dolphin and the beluga whale was $+5^\circ$ above the horizontal plane. For the false killer whale, 49% of the beam axis was at 0° and 32% at -5° . The four beam patterns for the false killer whale indicate that, like a linear transducer, the lower the frequency the wider the beam pattern. The type I signal has a peak frequency of about 30 kHz and has the widest beam. However, even though the peak frequency of the type IV signal is about 3.5 times higher than the type I signal, the beam does not seem to be substantially larger. This property can be used when discussing lower-frequency whistle signals to suggest that whistle signals are also emitted in a beam.

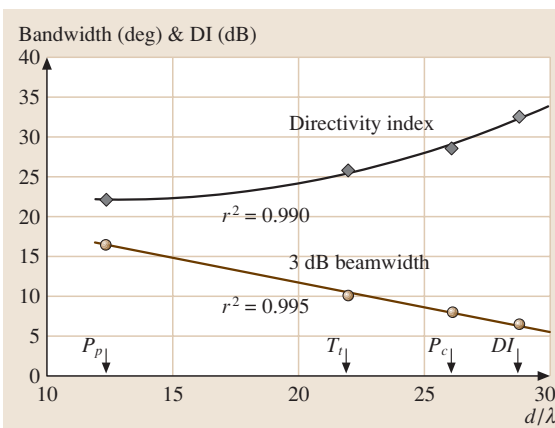


Fig. 20.13 Transmission directivity index and 3 dB beam width for four odontocetes. The directivity index and beam width for *Tursiops truncatus* and *delphinapterus leucas* came from Au [20.39] and for *pseudorca crassidens* after Au et al. [20.52]. The wavelength λ corresponds to the average peak frequency of the animals' echolocation signals. The directivity index is fitted with a second-order polynomial curve the the beam width is fitted with a linear curve (after Au et al. [20.70])

The only transmission beam pattern for a non-whistling odontocete, a *phocoena phocoena*, was measured by Au et al. [20.70]. Their results are shown in Fig. 20.12 in both the horizontal and vertical planes. One of the obvious difference between the beam patterns in Fig. 20.12 and those in Figs. 20.10 and 20.11 is the width of the beam. Although the harbor porpoise emitted the highest-frequency signals, its small head size caused the beam to be wider than for the other animals. The beam patterns of Figs. 20.10–20.12 were inserted into (20.1) and numerically evaluated to estimate the corresponding directivity index for *tursiops* and *delphinapterus* [20.39] and for *pseudorca* by Au et al. [20.52] and for *phocoena* [20.70], and the results are shown in Fig. 20.13 plotted as a function of the ratio of the head diameter (at the blow hole) of the subject and the average peak frequency of the animals echolocation signal. Also shown in Fig. 20.13 are the 3 dB beam width, where the 3 dB beam width in the vertical and horizontal planes were averaged.

The second-order polynomial fit of the directivity index is given by the equation

$$DI = 28.89 - 1.04 \left(\frac{d}{\lambda} \right) + 0.04 \left(\frac{d}{\lambda} \right)^2. \quad (20.9)$$

The linear fit of the 3 dB beam width data is given by the equation

$$BW = 23.90 - 0.60 \left(\frac{d}{\lambda} \right). \quad (20.10)$$

The results of Fig. 20.13 provides a way of estimating the directivity index and 3 dB beam width of other odontocetes by knowing their head size and the peak frequency of their echolocation signals.

20.3 Odontocete Acoustic Communication

Members of the *Odontocete* suborder are an intriguing example of the adaptability of social mammalian life to the aquatic habitat. Most odontocetes, particularly marine dolphins, live in groups ranging from several to hundreds of animals in size, forage cooperatively, develop hierarchies, engage in alloparental care and form strong pair bonds and coalitions between both kin and non-kin alike (see [20.71–73] for a review of the literature on dolphin societies). These social traits are analogous to patterns found in many avian and terrestrial mammalian species. It is not surprising, therefore, that odontocetes mediate much social information via communication. Some river dolphins are usually found as solitary individuals or mother–calf pairs although they may occasionally congregate into larger groups.

Odontocetes communicate through a combination of sensory modalities that include the visual, tactile, acoustic and chemosensory channels [20.74]. Visual signals in the form of postural displays are thought to convey levels of aggression, changes in direction of movement, and affiliative states [20.72, 75]. Tactile interactions vary in purpose from sexual and affiliative signals to expressions of dominance and aggression [20.76, 77]. Although not well documented yet, it is thought that a derivative of chemosensory perception, termed *quasiolfaction* allows dolphins to relay chemical messages about stress and reproductive status [20.78, 79]. However, it is the acoustic communication channel in particular that is believed to be the main communication tool that enables odontocetes to function cohesively as groups in the vast, visually limited environment of the open sea [20.80]. Examining how odontocetes have adapted their use of sound is therefore an important step to understanding how social marine mammal life evolved in the sea and how it has found a way to thrive in a habitat so drastically different from our own.

When compared to all that has been learned about dolphin echolocation over the past several decades, sur-

prisingly little is still known about how dolphins and other odontocetes use acoustic signals for communication. A major reason for this is that it is very difficult to observe the acoustic and behavioral interactions between the producer and the receiver(s) of social signals in the underwater environment. Sound propagation in the sea makes even a simple task like identifying the location of a sound source very challenging for air-adapted listeners. Therefore, matching signals with specific individuals and their behavior in the field is problematic without the use of sophisticated recording arrays [20.57, 76, 81, 82], or directional transducers. In addition, many questions remain unanswered about the nature of social signals themselves. Much still remains unknown about the functional design of dolphin social sounds. This is largely due to the fact that most species specialize in producing and hearing sounds with frequencies well beyond the limits of the human hearing range. Limitations in the technology available to study social signaling in the field have until recently restricted most analyses to the human auditory bandwidth (< 20 kHz). Yet, despite these significant challenges, a great deal of progress has been made in our understanding of odontocete acoustic communication. Rapidly advancing technologies are contributing greatly to our ability to study social signaling both in the field and in the laboratory. The emerging picture reveals that odontocetes have adapted their acoustic signaling to fit the aquatic world in a remarkably elegant way.

Another interesting characteristics of the beam pattern measurement on the *phocoena phocoena* is that the off-axis signals are not distorted in comparison to the on-axis signal. This is consistent with narrow-band signals whether for a linear technological transducer or a live animal. Therefore, measurements of echolocation signals of non-whistling odontocetes in the field can be performed much easier than for whistling odontocetes.

20.3.1 Social Acoustic Signals

Odontocetes have evolved in both marine and freshwater habitats for over 50 million years. Over such a long period of adaptive radiation one might expect that a variety of signaling strategies would have evolved among the approximately 65 species of small toothed whales and dolphins. Yet, remarkably, the vast majority of these species have either conserved or converged on the pro-

duction of two types of sounds: whistles and short pulse trains.

Whistles

Whistles are frequency- and amplitude-modulated tones that typically last anywhere from 50 ms to 3 s or more, as illustrated in Fig. 20.14. They are arguably the most variable signals produced by dolphins. Both within and across species they range widely in duration, bandwidth and degree of frequency modulation. How whistles are used in communication is an ongoing topic of debate among researchers, but most agree that they play an important role in maintaining contact between dispersed individuals and are important in social interactions [20.85].

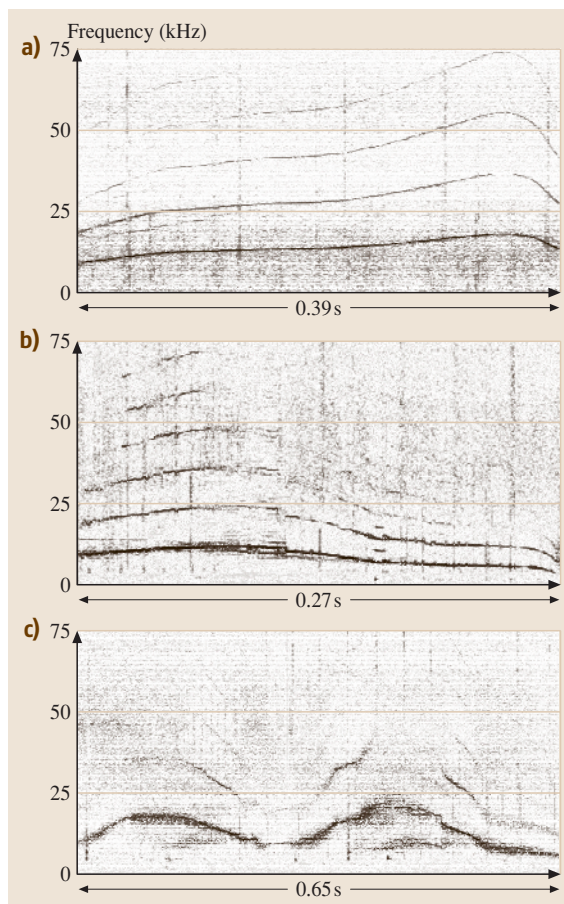


Fig. 20.14a–c Variations in whistle forms produced by Hawaiian spinner dolphins (a) and Atlantic spotted dolphins (b), (c) exhibiting multiple harmonics (after Lammers et al. [20.83, 84])

Dolphin whistles exhibit both species and geographic specificity [20.86–90]. Differences are greatest between distantly related taxa and between species of different size. As a general rule, larger species tend to produce whistles with lower fundamental frequencies than smaller ones [20.88]. Geographic variations within a species are usually smaller than interspecific differences [20.87], but some species do develop regional dialects between populations [20.89, 90]. These dialects tend to become more pronounced with increasing geographic separation. In addition, pelagic species tend to have whistles in a higher-frequency range and with more modulation than coastal and riverine species [20.86, 88]. Such differences have been proposed as species-specific reproductive-isolating characteristics [20.86], as ecological adaptations to different environmental conditions and/or resulting from restrictions imposed by physiology [20.88]. On the other hand, it must also be noted that numerous whistle forms are also shared by both sympatric and allopatric species [20.91]. The communicative function of shared whistle forms is unknown, but it is intriguing as it suggests a further tendency towards a convergence in signal design.

Dolphins produce whistles with fundamental frequencies usually in the human audible range (below 20 kHz). However, whistles typically also have harmonics (Fig. 20.14), which occur at integer multiples of the fundamental and extend well beyond the range of human hearing [20.84]. Harmonics are integral components of tonal signals produced by departures of the waveform from a sinusoidal pattern. Dolphin whistle harmonics have a *mixed directionality* property, which refers to the fact they become more directional with increasing frequency [20.83, 92]. It has been proposed that this signal feature functions as a cue, allowing listening animals to infer the orientation and direction of movement of a signaling dolphin [20.83, 92]. Harmonics may therefore be important in mediating group cohesion and coordination.

Burst Pulses

In addition to whistles, most odontocetes also produce pulsed social sounds known as *burst pulse* signals. Burst pulse signals are broadband click trains similar to those used in echolocation but with inter-click intervals of only 2–10 ms [20.93]. Because these intervals are considerably shorter than the processing period generally associated with echolocation and because they are often recorded during periods of high social activity, burst pulse click trains are thought instead to play an important role in communication.

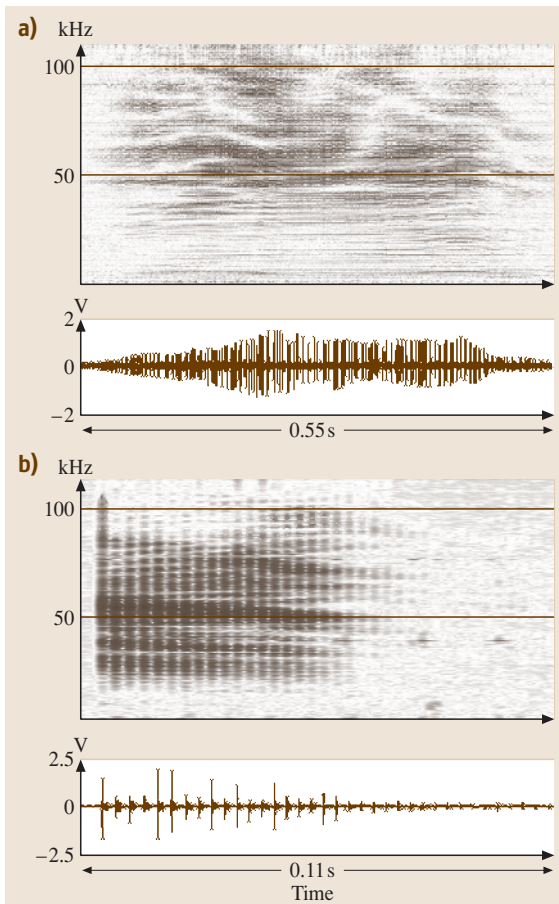


Fig. 20.15a,b Examples of (a) high-quantity and (b) low-quantity burst pulses produced by Atlantic spotted dolphins (*stenella frontalis*). Click train *a* has 255 clicks with mean ICI (interclick interval) of 1.7 ms. Click train *b* has 35 clicks with a mean ICI of 2.9 ms (after *Lammers et al.* [20.83,84])

Burst pulses vary greatly in the inter-pulse interval and in the number of clicks that occur in a train, which can number anywhere from three to hundreds of pulses, as depicted in Fig. 20.15. This variation gives them distinctive aural qualities. Consequently, burst pulse sounds have been given many subjective labels, including *yelps* [20.94], *cracks* [20.95], *screams* [20.96] and *squawks* [20.97]. Their production has been reported in a variety of odontocete species including: the Atlantic bottlenose dolphin (*tursiops truncatus*) [20.95], the Hawaiian spinner dolphin (*stenella longirostris*) [20.72], the Atlantic spotted dolphin (*stenella frontalis*) [20.98], the narwhal (*monodon monoceros*) [20.99], Hector's dolphin

(*cephalorhynchus hectori*) [20.100], the pilot whale (*globicephala melaena*) [20.101], and the harbor porpoise (*phocoena phocoena*) [20.101]. To date, much remains unknown about how burst pulses function as communication signals. It is generally believed that they play an important role in agonistic encounters because they are commonly observed during confrontational head-to-head behaviors between individuals [20.95, 102–104]. However, some authors have suggested they may represent emotive signals in a broader sense [20.97, 105, 106], possibly functioning as graded signals [20.107].

Given that dolphins have temporal discrimination abilities well within the range required to resolve individual clicks in a burst pulse [20.39, 108], it is possible that the quantity of clicks and their temporal spacing could form an important basis for communication. However, as with whistles, no data presently exist on the classification and discrimination tendencies of dolphins with respect to different burst pulses.

20.3.2 Signal Design Characteristics

Although much remains unknown about how odontocetes use acoustic signals for communication, the communicative potential of their signals can, in part, be inferred by considering the design characteristics that have been uncovered thus far. Signal features such as their detectable range, the production duty cycle, the identification level, the modulation potential and the form–content linkage provide useful clues about how odontocetes might use whistles and burst pulses.

The Active Space of Social Signals

The effective range of signals used for communication is generally termed the *active space*. *Janik* [20.109] investigated the active space of whistles produced by bottlenose dolphins in the Moray Firth, Scotland, using a dispersed hydrophone array to infer geometrically the location of signaling animals and establish the source level of their whistles. The mean source level was calculated to be $158 \text{ dB} \pm 0.6$ re $1 \mu\text{Pa}$, with a maximum recorded level of 169 dB. By factoring in transmission loss, ambient noise levels, the critical ratios and auditory sensitivity of the species involved the active space of an unmodulated whistle between 3.5 and 10 kHz in frequency was estimated to be between 20 and 25 km in a habitat 10 meters deep at sea state 0. At sea state 4 the estimated active space ranged from 14 to 22 km, while for whistles at 12 kHz it dropped to between 1.5 and 4 km. These estimations

were made for dolphins occurring in a relatively shallow, mostly mud-bottom, quiet environment. Presently, no data exist on the active space characteristics of delphinid whistles in pelagic waters and comparatively louder tropical near-shore environments. Similarly, no estimates have yet been made for the active space of burst pulses.

The Duty Cycle of Social Signals

Duty cycle refers to the proportion of time that any given signal or class of signals is *on* versus *off*. Signals can vary in the fine structure of their temporal patterning (e.g. duration), in their temporal spacing within a bout, and in their occurrence within a larger cyclical time frame, such as a 24 hour day. Each of these aspects of the temporal delivery of signals carries its own implication for communication. Fine-scale characteristics can define the nature of the signal itself and provide information about its relationship to other signals as well as constraints associated with its mechanism of production. The occurrence and timing of a signal within a bout can help convey information about the urgency of a situation, the level of arousal, the fitness of an individual and can assist the receiver in the task of localization. Finally, the periodicity of signals over hours or days can be an indicator of variables such as activity levels and reproductive state.

Murray et al. [20.110] investigated the fine-scale duty-cycle characteristics of delphinid social signals. Using a captive false killer whale (*pseudorca crassidens*) as their subject, they examined the temporal relationship between the units of a click train (individual clicks) and tonal signals. Their analysis revealed that false killer whales modulate the temporal occurrence of clicks to the point of grading them into a continuous wave (CW) signal such as a whistle. This finding was interpreted as evidence that *pseudorca* may employ graded signaling for communication (a topic discussed in more detail below), as well as to suggest that clicks and whistles are produced by the same anatomical mechanism.

The timing of signals within a bout has not been investigated with much success among delphinids. The primary obstacle towards this line of work has been the difficulty of identifying the signaler(s) involved for even short periods of time under field conditions. Early work by Caldwell and Caldwell [20.111] on a group or four naïve captive common dolphins (*delphinus delphis*) suggests that whistle exchanges do have temporal structure. In whistling bouts involving more than one signaler, the onset of a whistle specific to an individual was followed within two seconds by that of another. Furthermore, ini-

tiation of a whistle by two animals within 0.3 s of one another always resulted in the inhibition of one of them, with some individuals deferring more than others. Initiations separated by 0.4–0.5 s caused inhibition less frequently while those longer than 0.6 s resulted in almost no inhibition. Repeated whistles produced without an intervening response by another animal were usually delayed by less than one second. Thus, the duty cycle of whistling bouts and chorusing behavior among common dolphins does appear to follow certain temporal rules, but their significance is not clear.

Periodicity in social signaling has been investigated in captive bottlenose dolphins and common dolphins [20.112–114], as well as free-ranging spinner dolphins (*stenella longirostris*) [20.72] and common dolphins [20.115]. In the captive studies, signaling activity was linked to feeding schedules, nearby human activities and responses to different forms of introduced stress [20.113]. For spinner and common dolphins in the wild, the occurrence of social acoustic signals was highest at night, when both species were foraging, and lowest in the middle of the day.

The Identification Level of Social Signals

The role of delphinid whistles as individual-specific signals has been the focus of more scientific attention than any other aspect of their social acoustic signaling. Caldwell and Caldwell [20.116] were the first to propose that individual dolphins each possess their own distinct *signature* whistle. The idea was borne out of the observation that recently captured dolphins each produce a unique whistle contour that makes up over 90% of the individual's whistle output. Since being proposed, the so-called *signature whistle hypothesis* has emerged as the most widely accepted explanation for whistling behavior among dolphins. The idea has received support from numerous studies involving captive and restrained animals [20.85, 117–121] as well as from field studies of free-ranging animals [20.97, 122, 123]. Some, however, have argued that a simple signature function for dolphin whistling cannot account for the diversity of signals observed in socially interactive dolphin groups [20.124, 125]. While not denying the presence of signature whistles per se, these authors have argued that the large percentage of stereotyped signature signals observed in other studies may be an artifact of the unusual circumstances under which they were obtained (isolation, temporary restraint, separation, captivity). The debate over the prevalence of signature whistles among captive and free-ranging dolphins remains a contested topic in the

literature and at scientific meetings. On the other hand, no evidence or formal discussions presently exist suggesting burst pulse signals carry any individual-specific information.

The Modulation Potential of Social Signals

The modulation potential describes the amount of variation present in any given signal as measured by its position along a scale from stereotyped to graded signaling [20.126]. Stereotyped signals are repeats of structurally identical forms and vary discretely between one another. They are used most often for communication when the prospect of signal distortion is high, such as in noisy or reverberant environments or for communicating over long ranges. Graded signals have more variants than stereotyped ones and are encoded by changing one or more signal dimensions. These can include intensity, repetition rate and/or frequency and amplitude modulation. Graded signals are usually employed when a continuous or relative condition must be communicated in a favorable propagation environment.

Many studies to date have made an a priori assumption that dolphin signaling is categorical in nature, with signals belonging to mutually exclusive classes on the basis of their shared similarities. Some evidence in support of this assumption comes from the signature-whistle hypothesis work, where restrained and isolated individuals are often observed producing highly stereotyped bouts of signaling. However, few data are presently available to suggest how dolphins perceive and distinguish social signals [20.127]. Therefore, it is unclear whether an assumption based on the occurrence of signature whistles is broadly applicable towards other forms of social acoustic signaling (i. e. non-signature whistles and burst pulses).

A few studies have explored the occurrence of graded signaling in the communication of delphinids and the larger whales. *Taruski* [20.128] created a graded model for the whistles produced by North Atlantic pilot whales (*globicephala melaena*). He concluded that these signals could be arranged as a “continuum or matrix (of signals) from simple to complex through a series of intermediates” (*Taruski* [20.128] p. 349). *Murray et al.* [20.110], examining the signals of a captive false killer whale (*Pseudorca crassidens*), came to a similar conclusion and proposed that *Pseudorca* signals were also best represented along a continuum of signal characteristics, rather than categorically. Finally, *Clark* [20.129], examining the “call” signals of southern right whales (a mysticete),

made the observation that “... the total repertoire of calls is best described as a sequence of inter-graded types along a continuum” (*Taruski* [20.128] p. 1066). Therefore, graded signaling may well play a role in odontocete communication. Controlled perceptual experiments and a better understanding of the acoustic environment dolphins inhabit are needed to test how odontocetes discriminate and classify social sounds.

The Form–Content Linkage of Social Signals

The degree to which the form of a signal is linked to its content depends on how information is coded and on proximate factors associated with the signal’s production. The relationship between a signal’s structural form and its message can range from being rather arbitrary to tightly linked to a specific condition [20.126]. Among odontocetes, a clear relationship between signal form and content has only been demonstrated for signature whistles (discussed above). Dolphins have been experimentally shown to be capable of labeling objects acoustically (also known as vocal learning), as well as mimicking model sounds following only a single exposure [20.130]. Additional evidence of vocal learning exists from culturally transmitted signals in the wild [20.131] and in captivity [20.132], as well as from the spontaneous production of acoustic labels in captivity [20.127]. Context-specific variations in signature whistle form have also been demonstrated [20.121]. However, to date, no semantic rules have been identified for naturally occurring social signals among odontocetes.

Geographic Difference and Dialect

There is a distinct difference between geographical difference and dialect. Geographical differences are associated with widely separated populations that do not normally mix. Dialect is best reserved for sound emission differences on a local scale among neighboring populations which can potentially intermix [20.133]. Geographic variations are generally considered to result from acoustic adaptations to different environments, or a functionless byproduct of isolation and genetic divergence caused by isolation [20.134]. The functional significance of dialects is controversial, with some maintaining that dialects are epiphenomena of song learning and social adaptation, whereas others believe that they play a role in assorted mating and are of evolutionary significance [20.134]. Dialects are known to occur in many species of birds [20.135] but appear to be very rare in mammals.

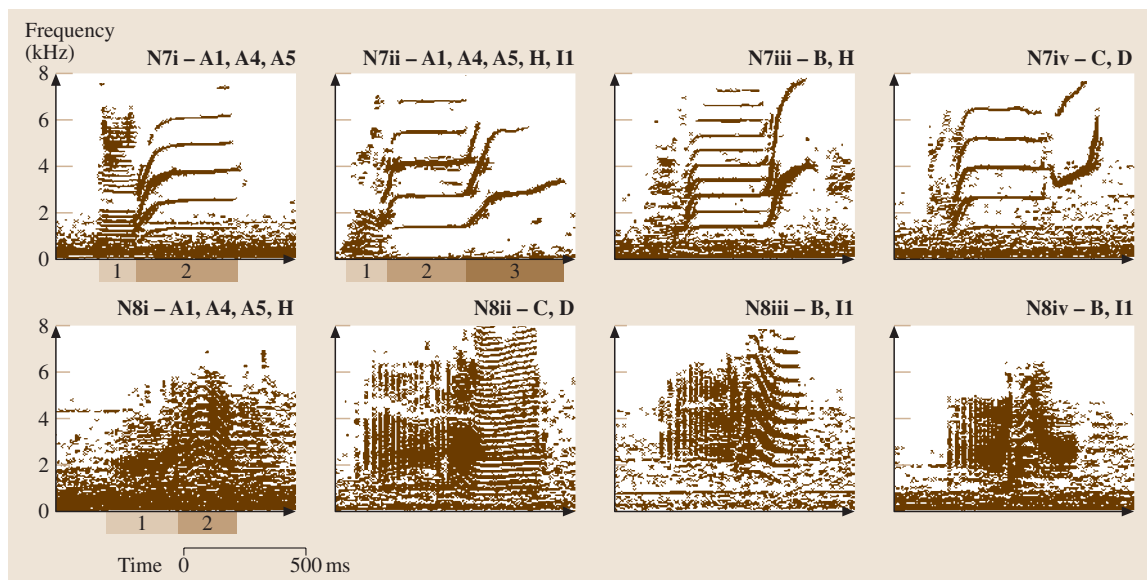


Fig. 20.16 Spectrograms of call types N7 and N8 for clan A. Above each spectrogram is the subtype identification and the pods that produce the variant, and below certain spectrograms are division marks separating calls into their component parts (after Ford [20.134]).

Killer Whale

Killer whales (*orcinus orca*) produce a specific type of burst pulse termed the *discrete call*. Discrete calls are thought to serve as contact calls between individuals, much like whistles in other odontocete species [20.136]. Discrete calls are population specific and even pod specific. The dialects of resident killer whales (*Orcinus orca*) in the coastal waters of British Columbia and Washington have been studied over a prolonged period by Ford and his colleagues [20.134, 137, 138]. They used photographic identification techniques, keying on unique natural markings on the whales to identify 16 pods or stable kin groups of 232 resident killer whales. Differences in acoustic behavior formed a system of related pod-specific dialects within the call tradition of each clan. Ford [20.134] has proposed that each clan is comprised of related pods that have descended from a common ancestral group and pod-specific repertoires probably serve to enhance the efficiency of acoustic communications within the group and act as behavioral indicators of pod affiliation.

Killer whale calls are typically made up of rapidly emitted pulses that to the human ear have a tonal quality [20.134]. Many calls have several abrupt shifts in pulse repetition rate allowing them to be divided into different segments or parts. Although all pods belonging to a clan share a number of calls, these calls were

often rendered in consistently different form by different pods. Also, certain pods produced calls that were not used by the rest of the clan. Such variations produced a set of related group-specific dialects within the call tradition of each clan.

Spectrograms of call types N7 and N8 are shown in Fig. 20.16. In this example, we can see that different pods produce similar but different versions of call type N7 and N8. Pods A1, A4 and A5 produced two versions of call type N7 and pod B and I1 produced two versions of call type N8. All of the spectrograms have two parts except for call type N7ii, which had three parts.

Ford [20.134] contended that pod-specific repertoires can be retained for periods in excess of 25 years. Discrete calls generally serve as signals for maintaining contact within the pod and that the use of repertoire of pod-specific calls enhances this function by conveying group identity and affiliation [20.134]. Killer whales, like most other small dolphins are able to learn and mimic a wide variety of sounds. Even from a young age, killer whale infants can selectively learn specific calls, especially the calls of their mothers. Bowles et al. [20.139] studied the development of calls of a captive-born killer whale calf and found that it learned and reproduced only the calls of its mother and ignored the calls of other killer whales in the same pool. Ford [20.134] also observed killer whales imi-

tating the call types of different pods, and even those from other clans. These instances were rare, but it does show a capacity for learning and mimicry of acoustic signals.

Sperm Whales

Sperm whales live in a matrilineal family unit where there exist cooperative behaviors including communal care of the young in ways similar to killer whales. The family units are very stable and females may live as long as 60–70 y [20.140]. One type of signals that sperm whales emit are denoted as codas, which are sequences of click signals that may be the primary means of acoustic communications for these animals [20.58]. *Weilgart* and *Whitehead* [20.141] recorded, for over a year, codas from a number of sperm whales around the South Pacific and in the Caribbean Sea. Photographic

identification also allowed them to assign recording sessions to particular groups. They found that the coda repertoire recorded from the same group on the same or different days were much more similar than those recorded from different groups in the same place. Groups recorded in the same place had more similar coda repertoire than those in the same broad area but different places. Groups from the same area were in turn marginally similar to those in the same ocean but different than those in different oceans. Coda class repertoires of groups in different oceans and in different areas within the same ocean were statistically significantly different. They concluded that strong group-specific dialects were apparently overlaid on weaker geographic variation. Sperm whales, killer whales and possibly bottlenose dolphins are the only cetaceans known to have dialects.

20.4 Acoustic Signals of Mysticetes

There are eleven species of mysticetes or baleen whales and sounds have been recorded from all but the pygmy right whale [20.142]. The vocalization of baleen whales can be divided into two general categories: (1) songs and (2) calls [20.142]. The calls can be further subdivided into three categories: (1) simple calls, (2) complex calls and (3) clicks, pulses, knocks and grunts [20.142]. Simple calls are often low-frequency, frequency-modulated signals with narrow instantaneous bandwidth that sound like moans if a recording is speeded up or slowed down, depending on the specific animal. Amplitude modulation and the presence of harmonics are usually part of a simple call, with most of the energy below 1 kHz. Complex calls are pulse-like broadband signals with a variable mixture of amplitude and/or frequency modulation. They sound like screams, roars, and growls, with most of the energy between 500–5000 Hz. Clicks, pulses, knocks and grunts are short-duration (< 0.1 s) signals with little or no frequency modulation. Clicks and pulses are very short (< 2 ms) signals with frequencies between 3–31 kHz, while grunts and knocks are longer (50–100 ms) signals in the 100–1000 Hz range [20.142].

20.4.1 Songs of Mysticete Whales

Songs are defined as “sequences of notes occurring in a regular sequence and patterned in time” [20.142]. Songs are easily discriminated from calls in most

instances. Four mysticetes species have been reported to produce songs; the blue whale (*balaenoptera musculus*) [20.143], the fin whale (*balaenoptera physalus*) [20.144, 145], the bowhead whale (*balaena mysticetus*) [20.15], and the humpback whale [20.146]. Songs of humpback whales have without a doubt received the most attention from researchers. Part of the reason for this is the relative ease for investigators to travel and do research in the summer grounds of humpback whales, especially in Hawaii in the Pacific and Puerto Rico in the Atlantic.

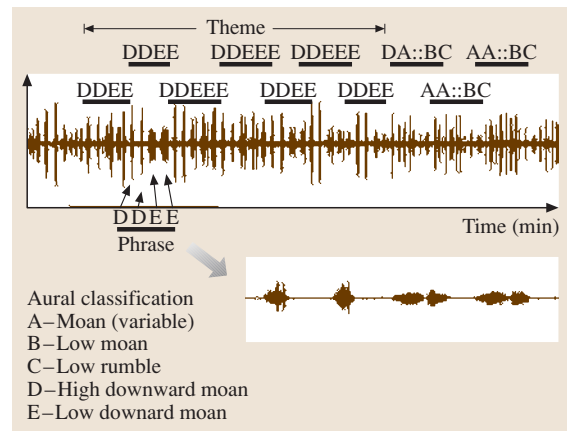


Fig. 20.17 Examples of two themes from a humpback whale song (after *Frankel* [20.36])

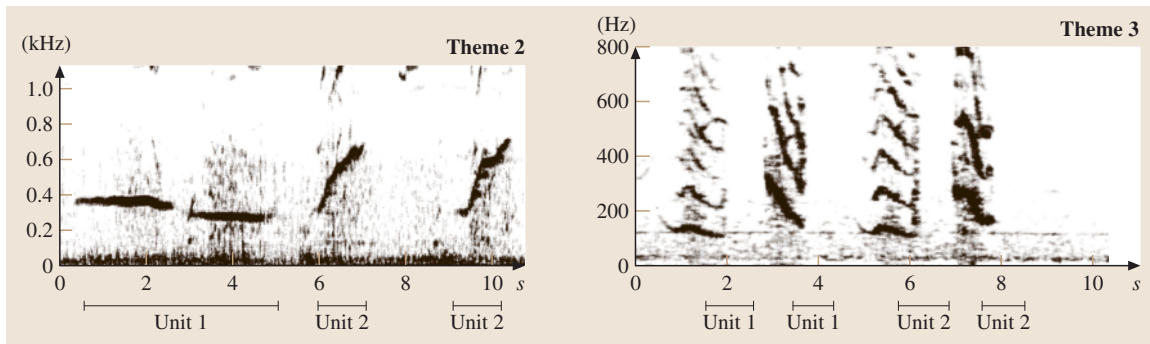


Fig. 20.18 An example of a portion of a humpback whale song. The individual pulse sounds are defined as units and units are aurally categorized based on how they sound. In this example, there are five units. Phrases are formed by a combination of units and themes are formed by a combination of phrases. The whole song consists of a combination of themes that are continuously repeated for the length of the song

Humpback Whale Songs

The list of studies involving humpback whale songs is long and extends from 1971 to the present time, *Helweg* et al. [20.147]. Although some songs may sound almost continuous to human listeners the basic units in a song are pulsed sounds. Songs are sung only by males and consist of distinct units that are produced in some sequence to form a phrase and a repeated set of phrases form a theme and repeated themes form a song. A song can last from minutes to hours depending on the disposition of the singer. An example of a portion of song is shown in Fig. 20.17. Example of two themes of a song in spectrogram format are shown in Fig. 20.18. The variation in frequency as a function of time is clearly shown in the figure.

Some general properties of songs and the whales that are singing are:

1. Songs from the North Pacific, South Pacific and Atlantic populations are different.
2. Singing peaks during the winter months when humpback whales migrate to warmer waters at lower latitudes.
3. Whales within a population sing the same basic song in any one year, although the song may undergo slight changes during a breeding season.
4. Changes in songs are not due to forgetting during the summer months, which are non-singing months, since songs recorded early in the winter breeding season are nearly the same as songs recorded late in the previous breeding season.
5. Songs from consecutive years are very similar but songs across nonconsecutive years will have fewer similarities.

6. Singers are most probably only males, since no females have been observed singing.
7. Some singing also occurs during the summer and fall.
8. Singing whales are often alone, although they have been occasionally observed singing in the presence of other humpback whales.
9. Singers tend to remain stationary. However, they have also been observed singing while swimming.

Other Mysticetes

Bowhead whales emit a variety of different types of simple and complex sounds that sound like moans to the human ear. They also emit sequential sounds that contain repeatable phrases that can be classified as songs during their spring migration [20.15] but not during the summer or autumn [20.148]. The bowhead song had just one theme with basically only two sounds repeated over and over. *Ljungblad* et al. [20.15] reported that songs were very tonal with clear pitch even though they were produced by pulsive moans, whereas *Cummings* and *Holliday* [20.149] described songs as sounding like raucous elephant roars and trumpeting in discrete repetitions or phrases that were put together to form longer sequences. Differences in the songs recorded by *Ljungblad* et al. [20.15] and by *Cummings* and *Holliday* [20.149] may be due to bowhead whales changing their songs from year to year.

The sounds from finback whales include single 20 Hz pulses, irregular series of 20 Hz pulses, and stereotyped 20 Hz signal bouts of repetitive sequences of 20 Hz pulses [20.145]. The 20 Hz signals are emitted in bouts that can last for hours. The pulse intervals in a bout were very regular. In general, signals are produced in

Table 20.2 Characteristics of mysticete whales vocalizations

Species of whales	Signal type	Frequency limits(HZ)	Dominant frequency (Hz)	Source level (dB re 1 μ Pa) at 1 m	References
Blue	FM moans	12.5 – 200	16 – 25	188	<i>Cummings, Thompson</i> [20.150], <i>Edds</i> [20.151]
	Songs	16 – 60	16– 60	–	<i>McDonald</i> et al. [20.152]
Bowhead	Tonal moans	25 –900	100 – 400	129 – 178	<i>Cummings, Holliday</i> [20.149]; <i>Wursig, Clark</i> [20.148]
	Pulses	25 –3500	152 – 185		<i>Cummings, Holliday</i> [20.149]; <i>Ljungblad</i> et al. [20.151]
	Songs	20 – 500	158 – 189		
Bryde's	FM moans	70 – 245	124 – 132	152 – 174	<i>Cummings</i> et al. [20.153]; <i>Edds</i> et al. [20.154]
	Pulsed moans	100 - 930	165 – 900	–	<i>Edds</i> et al. [20.154]
	Discrete pulses	700- 950	700 – 950	–	<i>Edds</i> et al. [20.154]
Finback	FM moans	14 – 118	20	160 – 186	<i>Watkins</i> [20.145], <i>Edds</i> [20.155], <i>Cummings, Thompson</i> [20.156]
	Tonals	34 – 150	34 – 150	–	<i>Edds</i> [20.155]
	Songs	17 – 25	17 – 25	186	<i>Watkins</i> [20.145]
Gray	Pulses	100 – 2000	300 – 825	–	<i>Dalheim</i> et al. [20.157]; <i>Crane</i> et al. [20.158]
	FM moans	250 – 300	250 – 300	152	<i>Cummings</i> et al. [20.159]; <i>Dalheim</i> et al. [20.157]
	LF-FM-moans	125 – 1250	< 430	175	<i>Cummings</i> et al. [20.159]; <i>Dalheim</i> et al. [20.157]
	PM pulses	150 – 1570	225 – 600	–	<i>Cummings</i> et al. [20.159]; <i>Dalheim</i> et al. [20.157]
	Complex moans	35 – 360	35 – 360	–	<i>Cummings</i> et al. [20.159]
Humpback	Grunts (pulse & FM)	25 – 1900	25 – 1900	176	<i>Thompson</i> et al. [20.160]
	Pulses	25 – 89	25 – 80	144 – 174	<i>Thompson</i> et al. [20.160]
	Songs	30 – 8000	120 – 4000	–	<i>Payne, Payne</i> [20.161]
Minke	FM tones	60 – 130	60 – 130	165	<i>Schevill, Watkins</i> [20.162], <i>Winn, Perkins</i> [20.163]
	Thumps	100 – 200	100 – 200	–	<i>Winn, Perkins</i> [20.163]
	Grunts	60 – 140	60 – 140	151 – 175	<i>Winn, Perkins</i> [20.163]
	Ratchets	850 – 6000	850	–	<i>Winn, Perkins</i> [20.163]
Right-N	Moans	< 400	–	–	<i>Schevill, Watkins</i> [20.162]
Right-S	Tonal	30 – 1250	160 – 500	–	<i>Cummings</i> et al. [20.164], <i>Clark</i> [20.129, 165]
	Pulses	30 – 2200	50 – 500	172 – 187	<i>Cummings</i> et al. [20.164], <i>Clark</i> [20.129, 165]
Sei	FM sweeps	1500 – 3500	1500 – 3500	–	<i>Knowlton</i> et al. [20.166]

a relatively regular sequence of repetitions at intervals ranging from about 7–26 s, with bouts that can last as long as 32.5 h. During a bout, periodic rests averaged about 115 s at roughly 15 min intervals and sometimes longer irregular gaps between 20 and 120 min were observed. There was also some variability in the 20 Hz signals in that they were never exactly replicated.

The songs of the blue whales (*balaenoptera musculus*) have been observed by a number of researchers [20.143, 152, 167]. A typical two-part blue

whale song time series and corresponding spectrogram is shown in Fig. 20.18. The spectrogram of the first part of the two part song had six spectral lines separated by about 1.5 Hz. This type of spectrogram is typically generated by pulses. *Cummings* and *Thompson* [20.150] previously reported on the pulsive nature of some blue whale moans. The second part of the song was tonal in nature with a slight FM down sweep varying from 19 Hz to 18 Hz in the first 3–4 s. The 18 Hz tone is then carried until the last 5 s when there is an abrupt step down to

17 Hz. The amplitude modulation in the second part of the song was probably caused by multi-path propagation of the signal from the whale to the hydrophones. These two-part songs basically follow a pattern of a 19 s pulsive signal followed by a 24.5 s gap and a 19 s monotonic signal [20.152, 167].

Calls of Mysticete Whales

The calls of mysticete whales have been the subject of much research over the past three decades. As with dolphin sounds, there is also a lack of any standard nomenclature for describing emitted sounds. Similar calls are often given different names by different researchers. A summary of some of the acoustic properties of the different baleen whales is indicated in Table 20.2. Calls and songs are most likely used for some sort

of communication, however, at this time the specific meanings of these sounds are not known. It is extremely difficult to study the context and functions of baleen whale vocalization. The sounds of mysticete whales have also been summarized nicely by Richardson et al. [20.34]. Instead of discussing the characteristics of various sounds, the properties of calls are summarized in Table 20.2. The calls of mysticete whales are mainly in the low-frequency range, from an infrasonic frequency of about 12.5 Hz for the blue whale to about 3.5 kHz for the sei whale. There are a variety of different types of calls, from FM tones to moans, grunts and discrete pulses. How these sounds are used by whales is still an open question since it is often very difficult to observe behavior associated with different calls.

20.5 Discussion

Cetaceans use a wide variety of sounds from brief echolocation signals used by dolphins having durations less than 100 μ s to very long duration songs that can last for hours by are emitted by humpback whales. The range of frequency is also very large, from low-frequency (infrasonic) sounds between 10–20 Hz used by blue and finback whales to high-frequency echolocation signals that extend to 130–140 kHz or perhaps higher (see earlier mention of 180 kHz). It is quite clear that acoustics is important in the natural history of cetaceans since all species regularly emit sounds throughout their daily routine. Yet, it is not at all clear how sounds are used by these animals. The difficulty in observing the behavior of these animals has made it difficult to attach any function to a particular or specific sound. It is nearly impossible to determine a one-to-one relationship between the reception or transmission of a specific sound to specific behavioral response. There are many possible functions of sounds, some of which may include providing contact information in a population of animals, signaling alarm or warning of approaching predators, attracting potential mates, echolocation for prey detection and discrimination while foraging, a way of establishing a hierarchy, providing individual identification, and a method for disciplining juveniles. Although researchers have not been successful in uncovering the role or function of specific sounds in any cetacean species, researchers should not be discouraged but should be innovative and imaginative in designing experiments that can be conducted in the wild to delve deeper into this problem. Even with

echolocation sounds, there are many unanswered questions. It seems logical that echolocation sounds are used to detect and discriminate prey and to navigate, yet we still know very little about how often they are emitted during a daily routine for dolphins in the field.

In this chapter, we have seen that the characteristics of the sounds emitted by cetaceans depends a lot on the size of the animals. Therefore the active space of different species is indirectly related to the size of the animals since the amount of sound absorption by

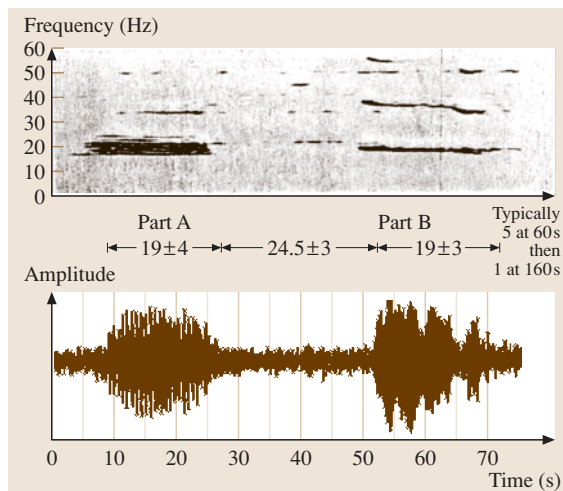


Fig. 20.19 Time series and spectrogram of a typical blue whale song (after [20.152])

sea water increases with frequency. Dolphins and small whales usually emit echolocation signals that can have peak frequencies up to 120–140 kHz and whistles between 10–20 kHz. These signals are not meant to travel large distances so that the active space is rather small, tens of meters for echolocations and burst pulse signals and several hundred meters for whistles. These signals will certainly propagate to much shorter distances than the low-frequency signals used by many of the baleen whales. The sound pressure level (SPL) of an emitted signal at any range from the animal is given by the equation

$$\text{SPL} = \text{SL} - \text{geometric spreading loss} - \alpha R, \quad (20.11)$$

where SL is the source level in dB, α is the sound absorption coefficient in dB/m and R is the distance the sound has traveled. The geometric spreading loss does not depend on frequency but is affected by the sound velocity profile, the depth of the source and the receiver. The most severe geometric spreading loss is associated with spherical spreading loss in which the amount of geometric spreading loss is equal to $20 \log R$. The least severe geometric spreading loss is associated with sound channels, such as the sound fixing and ranging (SOFAR) channel. In order to gain an appreciation of the effects of absorption losses for different types of cetacean signals, $-\alpha R$ in (20.9) was calculated as a function of range and the results are shown in Fig. 20.20. The results indicate that the low-frequency sounds used by baleen whales do not suffer as much absorption loss as the sounds of small odontocetes. Therefore, baleen whale signals can propagate long distances if some type of channel is present in the water column.

References

- 20.1 S.H. Ridgway: Who are the Whales, *Bioacoust.* **8**, 3–20 (1997)
- 20.2 B. Møhl, W.W.L. Au, J. Pawloski, P.E. Nachtigall: Dolphin hearing: Relative sensitivity as a function of point of application of a contact sound source in the jaw and head region, *J. Acoust. Soc. Am.* **105**, 3421–3424 (1999)
- 20.3 T.H. Bullock, A.D. Grinnell, E. Ikezono, K. Kameda, Y. Katsuki, M. Nomoto, O. Sato, N. Suga, K. Yanagisawa: Electrophysiological studies of central auditory mechanisms in Cetaceans, *Z. Vergl. Phys.* **59**, 117–316 (1968)
- 20.4 J.G. McCormick, E.G. Wever, J. Palin, S.J.H. Ridgway: Sound conduction in the dolphin ear, *J. Acoust. Soc. Am.* **48**, 1418–1428 (1970)
- 20.5 K.S. Norris: The evolution of acoustic mechanisms in odontocete cetaceans. In: *Evolution and Environment*, ed. by E.T. Drake (Yale Univ. Press, New Haven 1968) pp. 297–324
- 20.6 J.L. Aroyan: Three-dimensional modeling of hearing in *Delphinus delphis*, *J. Acoust. Soc. Am.* **110**, 3305–3318 (2001)
- 20.7 W.W.L. Au: Hearing in whales and dolphins: An overview. In: *Hearing by Whales and Dolphins*, ed. by W.W.L. Au, A.N. Popper, R.R. Fay (Springer, Berlin, New York, 2000) pp. 1–42
- 20.8 W.W.L. Au: Echolocation in dolphins. In: *Hearing by Whales and Dolphins*, ed. by W.W.L. Au, A.N. Popper, R.R. Fay (Springer, Berlin, New York 2000) pp. 364–408

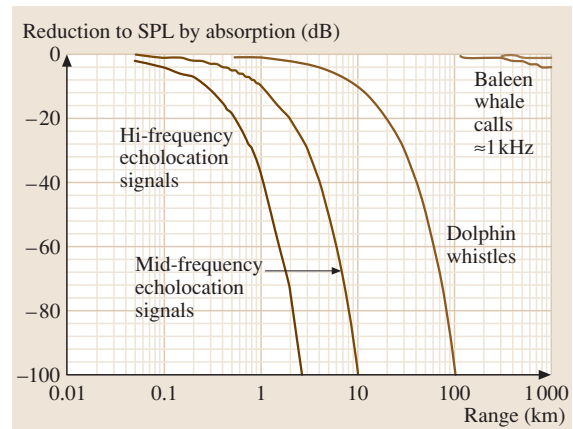


Fig. 20.20 Reduction to sound pressure level caused by sound absorption for different types of cetacean signals. The curve for the high-frequency echolocation signals was calculated at 120 kHz, and for the mid-frequency echolocation signals at 50 kHz. The curve for the dolphin whistle was calculated at 15 kHz. The baleen whale signal curve was determined at 1 kHz.

We have just scraped the top of the iceberg in regards to our understanding of cetacean acoustics. There is much to learn and understand about how these animals produce and receive sounds and how acoustics is used in their daily lives. The future looks extremely promising as new technology arrives on the scene that will allow researchers to delve into the many unanswered questions. As computer chips and satellite transmission tags get smaller and we apply state-of-the-art technologies to the study of cetaceans, our knowledge and understanding can but increase.

- 20.09 C.S. Johnson: Sound detection thresholds in marine mammals. In: *Marine Bioacoustics*, ed. by W. Tavolga (Pergamon, New York 1967) pp. 247–260
- 20.10 S. Andersen: Auditory sensitivity of the harbor porpoise, *Phocoena phocoena*. *Invest. Cetacea* **2**, 255–259 (1970)
- 20.11 R.A. Kastelein, P. Bunskoek, M. Hagedoorn, W.W.L. Au, D. de Haan: Audiogram of a harbor porpoise (*Phocoena phocoena*) measured with narrow-band frequency modulated signals, *J. Acoust. Soc. Am.* **112**, 334–344 (2002)
- 20.12 J.D. Hall, C.S. Johnson: Auditory thresholds of a killer whale, *J. Acoust. Soc. Am.* **51**, 515–517 (1971)
- 20.13 M.D. Szymanski, D.E. Bain, K. Kiehi, S. Pennington, S. Wong, K.R. Henry: Killer whale (*Orcinus orca*) hearing: Auditory brainstem response and behavioral audiograms, *J. Acoust. Soc. Am.* **106**, 1134–1141 (1999)
- 20.14 M.J. White Jr., J. Norris, D. Ljungblad, K. Baron, G. di Sciara: *Auditory thresholds of two beluga whales (Delphinapterus leucas)*. *HSWRI Tech. Rep. No. 78-109* (Hubbs Marine Research Institute, San Diego 1979)
- 20.15 D.K. Ljungblad, P.D. Scoggins, W.G. Gilmartin: Auditory thresholds of a captive eastern Pacific bottlenose dolphin, *Tursiops* spp., *J. Acoust. Soc. Am.* **72**, 1726–1729 (1982)
- 20.16 J. Thomas, N. Chun, W. Au, K. Pugh: Underwater audiogram of a false killer whale (*Pseudorca crassidens*), *J. Acoust. Soc. Am.* **84**, 936–940 (1988)
- 20.17 D. Wang, K. Wang, Y. Xiao, G. Sheng: Auditory sensitivity of a Chinese River Dolphin, *Lipotes vexillifer*. In: *Marine Mammal Sensory Systems*, ed. by J.A. Thomas, R.A. Kastelein, Aya Supin (Plenum, New York 1992) pp. 213–221
- 20.18 P.E. Nachtigall, W.W.L. Au, J.L. Pawloski, P.W.B. Moore: Risso's Dolphin (*Grampus griseus*) Hearing Thresholds in Kaneohe Bay, Hawaii. In: *Sensory Systems of Aquatic Mammals*, ed. by R.A. Kastelein, J.A. Thomas, P.E. Nachtigall (DeSpiel, Woerden 1995) pp. 49–53
- 20.19 M. Sauerland, D. Dehnhardt: Underwater Audiogram of a Tucuxi (*Sotalia fluviatilis guianensis*), *J. Acoust. Soc. Am.* **103**, 1199–1204 (1998)
- 20.20 R.A. Kastelein, M. Hagedoorn, W.W.L. Au, D. de Haan: Audiogram of a striped dolphin (*Stenella coeruleoalba*), *J. Acoust. Soc. Am.* **113**, 1130–1144 (2003)
- 20.21 R.R. Fay: *Hearing in Vertebrates: A Psychophysics Databook* (Hill-Fay Associates, Winnetka 1988)
- 20.22 A.W. Mills: On the Minimum Audible Angle, *J. Acoust. Soc. Am.* **30**, 237–246 (1958)
- 20.23 D.L. Renaud, A.N. Popper: Sound localization by the bottlenose porpoise *Tursiops truncatus*, *J. Exp. Biol.* **63**, 569–585 (1978)
- 20.24 A.W. Mills: Auditory localization. In: *Foundations of Modern Auditory Theory*, Vol. 2, ed. by J.V. Tobias (Academic, New York 1972) pp. 303–348
- 20.25 W.H. van Dudok Heel: Sound and Cetacea, *Netherlands J. Sea Res.* **1**, 407–507 (1962)
- 20.26 S. Andersen: Directional hearing in the harbor porpoise, *Phocoena phocoena*. *Invest. Cetacea* **2**, 261–263 (1970)
- 20.27 D.L. Renaud, A.N. Popper: Sound localization by the bottlenose porpoise, *tursiops truncatus*, *J. Exp. Biol.* **63**, 569–585 (1975)
- 20.28 W.W.L. Au, P.W.B. Moore: Receiving Beam Patterns and Directivity Indices of the Atlantic Bottlenose Dolphin *Tursiops truncatus*, *J. Acoust. Soc. Am.* **75**, 255–262 (1984)
- 20.29 D.S. Houser, J. Finneran, D. Carder, W. Van Bonn, C. Smith, C. Hoh, R. Mattrey, S. Ridgway: Structural and Functional Imaging of Bottlenose Dolphin (*Tursiops truncatus*) Cranial Anatomy, *J. Exp. Biol.* **207**, 3657–3665 (2004)
- 20.30 K.A. Zaytseva, A.I. Akopian, V.P. Morozov: Noise resistance of the dolphin auditory analyzer as a function of noise direction, *BioFizika* **20**, 519–521 (1975)
- 20.31 R.J. Urick: *Principles of Underwater Sounds for Engineers* (McGraw-Hill, New York 1980)
- 20.32 J.M. McCormick, M.G. Salvadori: *Numerical Methods in FORTRAN* (Prentice-Hall, Englewood Cliffs 1964),
- 20.33 D.R. Ketten: The marine mammal ear: specializations for aquatic audition and echolocation. In: *The Evolutionary Biology of Hearing*, ed. by D. Webster, R. Fay, A. Popper (Springer, Berlin, New York 1992) pp. 717–754
- 20.34 W.J. Richardson, C.R. Greene Jr., C.I. Malme, D.H. Thomson: *Marine Mammals and Noise* (Academic, San Diego 1995)
- 20.35 W.J. Richardson, B. Würsig, C.R. Greene Jr: Reactions of bowhead whales, *Balaena mysticetus*, to drilling and dredging noise in the Canadian Beaufort Sea, *Mar. Envr. Res.* **29**, 135–160 (1990),
- 20.36 A.S. Frankel: *Acoustic and visual tracking reveals distribution, song variability and social roles of humpback whales in Hawaiian waters*. *Ph.D. Dissertation* (Univ. Hawaii, Honolulu, HI 1994)
- 20.37 C.R. Ridgway: Electrophysiological experiments on hearing in odontocetes. In: *Animal Sonar*, ed. by P.E. Nachtigall, P.W.B. Moore (Plenum, New York 1980) pp. 483–493
- 20.38 S.H. Ridgway, D.A. Carder: Assessing hearing and sound production in cetaceans not available for behavioral audiograms: Experiences with sperm, pygmy sperm and gray whales, *Aquatic Mammals*. **27**, 267–276 (2001)
- 20.39 W.W.L. Au: *The Sonar of Dolphins* (Springer, Berlin, New York 1993)
- 20.40 S.H. Ridgway, D.A. Carder: Nasal pressure and sound production in an echolocating white whale, *Delphinapterus leucas*. In: *Animal Sonar: Processes and Performance*, ed. by P.E. Nachtigall,

- P.W.B. Moore (Plenum, New York 1988) pp. 53–60,
- 20.41 F.G. Wood: Discussion. In: *Marine Bio-Acoustics Vol. II*, ed. by W. Tavolga (Pergamon, Oxford 1964) pp. 395–396
- 20.42 K.S. Norris, G.W. Harvey: Sound transmission in the porpoise head, *J. Acoust. Soc. Am.* **56**, 659–664 (1974)
- 20.43 J.L. Aroyan, T.W. Cranford, J. Kent, K.S. Norris: Computer modeling of acoustic beam formation in *Delphinus delphis*, *J. Acoust. Soc. Am.* **95**, 2539–2545 (1992)
- 20.44 T.W. Cranford: In Search of Impulse sound sources in odontocetes. In: *Hearing by Whales and Dolphins*, ed. by W.W.L. Au, A.N. Popper, R.R. Fay (Springer, New York 2000) pp. 109–155
- 20.45 W.W.L. Au, R.W. Floyd, R.H. Penner, A.E. Murchison: Measurement of echolocation signals of the Atlantic bottlenose dolphin *Tursiops truncatus* Montagu, in Open Waters, *J. Acoust. Soc. Am.* **56**, 280–290 (1974)
- 20.46 W.E. Evans: Echolocation by marine delphinids and one species of fresh-water dolphin, *J. Acoust. Soc. Am.* **54**, 191–199 (1973)
- 20.47 W.W.L. Au, D.A. Carder, R.H. Penner, B.L. Scronce: Demonstration of adaptation in beluga whale echolocation signals, *J. Acoust. Soc. Am.* **77**, 726–730 (1985)
- 20.48 B.S. Gurevich, W.E. Evans: Echolocation discrimination of complex planar targets by the beluga whale (*Delphinapterus leucas*), *J. Acoust. Soc. Am.* **60**, 55 (1976)
- 20.49 C. Kamminga, H. Wiersma: Investigations on cetacean sonar V. The true nature of the sonar sound of *Cephaloryncus Commersonii*, *Aqua. Mamm.* **9**, 95–104 (1981)
- 20.50 C.W. Turl, D.J. Skaar, W.W.L. Au: The Echolocation Ability of the Beluga (*Delphinapterus leucas*) to detect Targets in Clutter, *J. Acoust. Soc. Am.* **89**, 896–901 (1991)
- 20.51 P.W.B. Moore, D.A. Pawloski: Investigations on the control of echolocation pulses in the dolphin (*Tursiops truncatus*). In: *Sensory Abilities of Cetaceans Laboratory and Field Evidence*, ed. by J.A. Thomas, R.A. Kastelein (Plenum, New York 1990) pp. 305–316
- 20.52 W.W.L. Au, J.L. Pawloski, P.E. Nachtigall: Echolocation signals and transmission beam pattern of a false killer whale (*Pseudorca crassidens*), *J. Acoust. Soc. Am.* **98**, 51–59 (1995)
- 20.53 J. Thomas, M. Stoermer, C. Bowers, L. Anderson, A. Garver: Detection abilities and signal characteristics of echolocating false killer whales (*Pseudorca crassidens*). In: *Animal Sonar Processing and Performance*, ed. by P.E. Nachtigall, P.W.B. Moore (Plenum, New York 1988) pp. 323–328
- 20.54 J.A. Thomas, C.W. Turl: Echolocation characteristics and range detection by a false killer whale *Pseudorca crassidens*. In: *Sensory Abilities of Cetaceans: Laboratory and Field Evidence*, ed. by J.A. Thomas, R.A. Kastelein (Plenum, New York 1990) pp. 321–334
- 20.55 W.W.L. Au, J.K.B. Ford, J.K. Horne, K.A. Newman-Allman: Echolocation signals of free-ranging killer whales (*Orcinus orca*) and modeling of foraging for chinook salmon (*Oncorhynchus tshawytscha*), *J. Acoust. Soc. Am.* **115**, 901–909 (2004)
- 20.56 W.W.L. Au, B. Würsig: Echolocation signals of dusky dolphins (*Lagenorhynchus obscurus*) in Kaikoura, New Zealand, *J. Acoust. Soc. Am.* **115**, 2307–2313 (2004)
- 20.57 W.W.L. Au, D. Herzing: Echolocation signals of wild Atlantic spotted dolphin (*Stenella frontalis*), *J. Acoust. Soc. Am.* **113**, 598–604 (2003)
- 20.58 W.A. Watkins, W.E. Schevill: Sperm whale codas, *J. Acoust. Soc. Am.* **62**, 1485–1490 (1977)
- 20.59 C. Levenson: Source level and bistatic target strength of sperm whale (*Physeter catodon*) measured from an oceanographic aircraft, *J. Acoust. Soc. Am.* **55**, 1100–1103 (1974)
- 20.60 L. Weilgart, H. Whitehead: Distinctive vocalizations from mature male sperm whales (*Physeter macrocephalus*), *Can. J. Zool.* **66**, 1931–1937 (1988)
- 20.61 B. Møhl, E. Larsen, M. Amundin: Sperm Whale Size Determination: Outlines of an Acoustic Approach. In: *Mammals in the Seas. Fisheries series No. 5, Mammals of the Seas*, Vol. 3 (FAO (Food and Agriculture Organization of the United Nations) Publications, Rome 1981) pp. 327–331
- 20.62 J.L. Dunn: Airborne Measurements of the Acoustic Characteristics of a Sperm Whale, *J. Acoust. Soc. Am.* **46**, 1052–1054 (1969)
- 20.63 W.A. Watkins: Acoustics and the behavior of sperm whales. In: *Animal Sonar Systems*, ed. by R.G. Busnel, J.F. Fish (Plenum, New York 1980) pp. 291–297
- 20.64 B. Møhl, M. Wahlberg, A. Heerfordt: A GPS-linked array of independent receiver for bioacoustics, *J. Acoust. Soc. Am.* **109**, 434–437 (2001)
- 20.65 B. Møhl, M. Wahlberg, P.T. Madsen, A. Heerfordt, A. Lund: The monopulsed nature of sperm whale clicks, *J. Acoust. Soc. Am.* **114**, 1143–1154 (2003)
- 20.66 W.W.L. Au, R.H. Penner, C.W. Turl: Propagation of beluga echolocation signal, *J. Acoust. Soc. Am.* **82**, 807–813 (1987)
- 20.67 R.A. Kastelein, W.W.L. Au, H.T. Rippe, N.M. Schooneman: Target detection by an echolocating harbor porpoise (*Phocoena phocoena*), *J. Acoust. Soc. Am.* **105**, 2493–2498 (1999)
- 20.68 W.W.L. Au, K.J. Snyder: Long-range Target Detection in Open Waters by an Echolocating Atlantic Bottlenose Dolphin (*Tursiops truncatus*), *J. Acoust. Soc. Am.* **68**, 1077–1084 (1980)
- 20.69 P.T. Madsen, D.A. Carder, K. Bedholm, S.H. Ridgway: Porpoise clicks from a sperm whale nose – convergent evolution of 130 kHz pulses in toothed whale sonars?, *Bioacoustics* **15**, 192–206 (2005)
- 20.70 W.W.L. Au, R.A. Kastelein, T. Ripper, N.M. Schooneman: Transmission beam pattern and echolocation

- signals of a harbor porpoise (*Phocoena phocoena*), *J. Acoustic. Soc. Am.* **106**, 3699–3705 (1999)
- 20.71 K.W. Pryor, K.S. Norris: *Dolphin Societies: Discoveries and Puzzles* (Univ. California Press, Berkeley 1991)
- 20.72 K.S. Norris, B. Würsig, R.S. Wells, M. Würsig: *The Hawai'ian Spinner Dolphin* (Univ. California Press, Berkeley 1994) p. 408
- 20.73 J. Mann, P.L. Tyack, H. Whitehead: *Cetacean societies: field studies of dolphins and whales* (Univ. Chicago Press, Chicago 2000)
- 20.74 L.M. Herman, W.N. Tavolga: The communication systems of cetaceans. In: *Cetacean Behavior: Mechanisms and Function*, ed. by L.M. Herman (Wiley-Interscience, New York 1980) pp. 149–209
- 20.75 K.W. Pryor: Non-acoustic communication in small cetaceans: glance touch position gesture and bubbles. In: *Sensory Abilities of Cetaceans*, ed. by J. Thomas, R. Kastelein (Plenum, New York 1990) pp. 537–544
- 20.76 K.M. Dudzinski: Contact behavior and signal exchange in Atlantic spotted dolphins (*Stenella frontalis*), *Aqua. Mamm.* **24**, 129–142 (1998)
- 20.77 C.M. Johnson, K. Moewe: Pectoral fin preference during contact in Commerson's dolphins (*Cephalorhynchus commersonii*), *Aqua. Mamm.* **25**, 73–77 (1999)
- 20.78 P.E. Nachtigall: Vision, audition and chemoreception in dolphins and other marine mammals. In: *Dolphin Cognition and Behavior: A Comparative Approach*, ed. by R.J. Schusterman, J.A. Thomas, F.G. Wood (Lawrence Erlbaum, Hillsdale 1986) pp. 79–113
- 20.79 V.B. Kuznetsov: Chemical sense of dolphins: quasi-olfaction. In: *Sensory Abilities of Cetaceans*, ed. by J. Thomas, R. Kastelein (Plenum, New York 1990) pp. 481–503
- 20.80 K.S. Norris, E.C. Evans III.: On the evolution of acoustic communication systems in vertebrates, Part I: Historical aspects. In: *Animal Sonar: Processes and Performance*, ed. by P.E. Nachtigall, P.W.B. Moore (Plenum, New York 1988) pp. 655–669
- 20.81 R.E. Thomas, K.M. Fristrup, P.L. Tyack: Linking the sounds of dolphins to their locations and behavior using video and multichannel acoustic recordings, *J. Acoust. Soc. Am.* **112**, 1692–1701 (2002)
- 20.82 K.R. Ball, J.R. Buck: A beamforming video recorder for integrated observations of dolphin behavior and vocalizations, *J. Acoust. Soc. Am.* **117**, 1005–1008 (2005)
- 20.83 M.O. Lammers, W.W.L. Au, D.L. Herzing: The broadband social acoustic signaling behavior of spinner and spotted dolphins, *J. Acoust. Soc. Am.* **114**, 1629–1639 (2003)
- 20.84 M.O. Lammers, W.W.L. Au: Directionality in the whistles of Hawai'ian spinner dolphins (*Stenella longirostris*): A signal feature to cue direction of movement?, *Mar. Mamm. Sci.* **19**, 249–264 (2003)
- 20.85 V.M. Janik, P.J.B. Slater: Context specific use suggests that bottlenose dolphin signature whistles are cohesion calls, *Anim. Behav.* **56**, 829–838 (1998)
- 20.86 W.W. Steiner: Species-specific differences in pure-tonal whistle vocalizations of five western north Atlantic dolphin species, *Behav. Ecol. Sociobiol.* **9**, 241–246 (1981)
- 20.87 L.E. Rendell, J.N. Matthews, A. Gill, J.C.D. Gordon, D.W. MacDonald: Quantitative analysis of tonal calls from five odontocete species, examining interspecific and intraspecific variation, *J. Zool.* **249**, 403–410 (1999)
- 20.88 W. Ding, B. Würsig, W.E. Evans: Comparisons of whistles among seven odontocete species. In: *Sensory Systems of Aquatic Mammals*, ed. by R.A. Kastelein, J.A. Thomas (De Spil, Woerden 1995) pp. 299–323
- 20.89 W. Ding, B. Würsig, W.E. Evans: Whistles of bottlenose dolphins: comparisons among populations, *Aqua. Mamm.* **21**, 65–77 (1995)
- 20.90 C. Bazua-Duran, W.W.L. Au: Geographic variations in the whistles of spinner dolphins (*Stenella longirostris*) of the Main Hawai'ian Islands, *J. Acoust. Soc. Am.* **116**, 3757–3769 (2004)
- 20.91 J.N. Oswald, J. Barlow, T.F. Norris: Acoustic identification of nine delphinid species in the eastern tropical Pacific Ocean, *Mar. Mamm. Sci.* **19**, 20–37 (2003)
- 20.92 P.J.O. Miller: Mixed-directionality of killer whale stereotyped calls: a direction-of-movement cue?, *Behav. Ecol. Sociobiol.* **52**, 262–270 (2002)
- 20.93 M.O. Lammers, W.W.L. Au, R. Aubauer: A comparative analysis of echolocation and burst-pulse click trains in *Stenella longirostris*. In: *Echolocation in Bats and Dolphins*, ed. by J. Thomas, C. Moss, M. Vater (Univ. Chicago Press, Chicago 2004) pp. 414–419
- 20.94 A.E. Puente, D.A. Dewsbury: Courtship and copulatory behavior of bottlenose dolphins (*Tursiops truncatus*), *Cetology* **21**, 1–9 (1976)
- 20.95 M.C. Caldwell, D.K. Caldwell: Intraspecific transfer of information via the pulsed sound in captive Odontocete Cetaceans. In: *Animal Sonar Systems: Biology and Bionics*, ed. by R.G. Busnel (Laboratoire de Physiologie Acoustique: Jouy-en-Josas, France 1967) pp. 879–936
- 20.96 S.M. Dawson: Clicks and communication: the behavioural and social contexts of Hector's dolphin vocalizations, *Ethology* **88**, 265–276 (1991)
- 20.97 D.L. Herzing: Vocalizations and associated underwater behavior of free-ranging Atlantic spotted dolphins, *Stenella frontalis* and bottlenose dolphin, *Tursiops truncatus*, *Aqua. Mamm.* **22**, 61–79 (1996)

- 20.98 M.C. Caldwell, D.K. Caldwell: Underwater pulsed sounds produced by captive spotted dolphins, *Stenella plagiodon*, *Cetology* **1**, 1–7 (1971)
- 20.99 J.K.B. Ford, H.D. Fisher: Underwater acoustic signals of the narwhal (*Monodon monoceros*), *Can. J. Zool.* **56**, 552–560 (1978)
- 20.100 S.M. Dawson: The high frequency sounds of free-ranging Hector's dolphins, *Cephalorhynchus hectori*, *Rep. Int. Whal. Comm. Spec. Issue* **9**, 339–344 (1988)
- 20.101 R.G. Busnel, A. Dziedzic: Acoustic signals of the Pilot whale *Globicephala melaena*, *Delphinus delphis* and *Phocoena phocoena*. In: *Whales, Dolphins and porpoises*, ed. by K.S. Norris (Univ. California Press, Berkeley 1966) pp. 607–648
- 20.102 N.A. Overstrom: Association between burst-pulse sounds and aggressive behavior in captive Atlantic bottlenose dolphins (*Tursiops truncatus*), *Zoo Biol.* **2**, 93–103 (1983)
- 20.103 B. McCowan, D. Reiss: Maternal aggressive contact vocalizations in captive bottlenose dolphins (*Tursiops truncatus*): wide-band, low frequency signals during mother/aunt-infant interactions, *Zoo Biol.* **14**, 293–309 (1995)
- 20.104 C. Bloomqvist, M. Amundin: High frequency burst-pulse sounds in agonistic/ aggressive interactions in bottlenose dolphins (*Tursiops truncatus*). In: *Echolocation in Bats and Dolphins*, ed. by J. Thomas, C. Moss, M. Vater (Univ. Chicago Press, Chicago, IL 2004) pp. 425–431
- 20.105 J.C. Lilly, A.M. Miller: Sounds emitted by the bottlenose dolphin, *Science* **133**, 1689–1693 (1961),
- 20.106 D.L. Herzing: *A Quantitative description and behavioral association of a burst-pulsed sound, the squawk, in captive bottlenose dolphins, Tursiops truncatus*, *Masters Thesis* (San Francisco State University, San Francisco 1988) p. 87
- 20.107 S.M. Brownlee: *Correlations between sounds and behavior in wild Hawai'ian spinner dolphins (Stenella longirostris)*. *Masters Thesis* (Univ. California, Santa Cruz 1983) p. 26
- 20.108 V.A. Vel'min, N.A. Dubrovskiy: The critical interval of active hearing in dolphins, *Sov. Phys. Acoust.* **2**, 351–352 (1976)
- 20.109 V.M. Janik: Source levels and the estimated active space of bottlenose dolphin (*Tursiops truncatus*) whistles in the Moray Firth, Scotland, *J. Comp. Psych.* **186**, 673–680 (2000)
- 20.110 S.O. Murray, E. Mercado, H.L. Roitblat: Characterizing the graded structure of false killer whale (*Pseudorca crassidens*) vocalizations, *J. Acoust. Soc. Am.* **104**, 1679–1688 (1998)
- 20.111 M.C. Caldwell, D.K. Caldwell: Vocalizations of naïve captive dolphins in small groups, *Science* **159**, 1121–1123 (1968)
- 20.112 W.A. Powell: Periodicity of vocal activity of captive Atlantic bottlenose dolphins: *Tursiops truncatus*, *Bull. Soc. Ca. Acad. Sci.* **65**, 237–244 (1966),
- 20.113 I.E. Sidorova, V.I. Markov, V.M. Ostrovskaya: Signalization of the bottlenose dolphin during the adaptation to different stressors. In: *Sensory Abilities of Cetaceans*, ed. by J. Thomas, R. Kastelein (Plenum, New York 1990) pp. 623–638
- 20.114 S.E. Moore, S.H. Ridgway: Whistles produced by common dolphins from the Southern California Bight, *Aqua. Mamm.* **21**, 55–63 (1995)
- 20.115 J.C. Goold: A diel pattern in vocal activity of short-beaked common dolphins, *Delphinus delphis*, *Mar. Mamm. Sci.* **16**, 240–244 (2000)
- 20.116 M.C. Caldwell, D.K. Caldwell: Individualized whistle contours in bottlenosed dolphins (*Tursiops truncatus*), *Nature* **207**, 434–435 (1965)
- 20.117 P.L. Tyack: Whistle repertoires of two bottlenose dolphins, *Tursiops truncatus*: mimicry of signature whistles?, *Behav. Ecol. Sociobiol.* **18**, 251–257 (1986)
- 20.118 M.C. Caldwell, D.K. Caldwell, P.L. Tyack: A review of the signature whistle hypothesis for the Atlantic bottlenose dolphin. In: *The Bottlenose Dolphin*, ed. by S. Leatherwood, R.R. Reeves (Academic, San Diego 1990) pp. 199–234
- 20.119 L.S. Sayigh, P.L. Tyack, R.S. Wells, M.D. Scott, A.B. Irvine: Signature differences in signature whistles production of free-ranging bottlenose dolphins *Tursiops truncatus*, *Behav. Ecol. Sociobiol.* **36**, 171–177 (1990)
- 20.120 L.S. Sayigh, P.L. Tyack, R.W. Wells, M.D. Scott, A.B. Irvine: Sex difference in signature whistle production of free-ranging bottlenose dolphins, *Tursiops truncatus*, *Behav. Ecol. Sociobiol.* **36**, 171–177 (1995)
- 20.121 V.M. Janik, G. Denhardt, T. Dietmar: Signature whistle variation in a bottlenosed dolphin, *Tursiops truncatus*, *Behav. Ecol. Sociobiol.* **35**, 243–248 (1994)
- 20.122 R.A. Smolker, J. Mann, B.B. Smuts: Use of signature whistles during separations and reunions by wild bottlenose dolphin mothers and infants, *Behav. Ecol. Sociobiol.* **33**, 393–402 (1993)
- 20.123 V.M. Janik: Whistle matching in wild bottlenose dolphins (*Tursiops truncatus*), *Science* **289**, 1355–1357 (2000)
- 20.124 B. McCowan, D. Reiss: Quantitative comparison of whistle repertoires from captive adult bottlenose dolphins (*Delphinidae*, *Tursiops truncatus*): A re-evaluation of the signature whistle hypothesis, *Ethology* **100**, 194–209 (1995)
- 20.125 B. McCowan, D. Reiss: The fallacy of 'signature whistles' in bottlenose dolphins: a comparative perspective of 'signature information' in animal vocalizations, *Anim. Behav.* **62**, 1151–1162 (2001)
- 20.126 J.W. Bradbury, S.L. Vehrencamp: *Principles of Animal Communication* (Sinauer Associates, Sunderland 1998) p. 882

- 20.127 D. Reiss, B. McCowan: Spontaneous vocal mimicry and production by bottlenose dolphins (*Tursiops truncatus*): Evidence for vocal learning, *J. Comp. Psychol.* **101**, 301–312 (1993)
- 20.128 A.G. Taruski: The whistle repertoire of the North Atlantic pilot whale (*Globicephala melaena*) and its relationship to behavior and environment. In: *Behavior of Marine Animals: Current Perspectives on Research. Vol. 3: Cetaceans*, ed. by H.E. Winn, B.L. Olla (Plenum, New York 1979) pp. 345–368
- 20.129 C.W. Clark: The acoustic repertoire of the southern right whale: A quantitative analysis, *Anim. Behav.* **30**, 1060–1071 (1982)
- 20.130 D.G. Richards, J.P. Wolz, L.M. Herman: Vocal mimicry of computer-generated sounds and vocal labeling of objects by a bottlenose dolphin, *Tursiops truncatus*, *J. Comp. Psych.* **98**, 10–28 (1984)
- 20.131 V.B. Deecke, J.K.B. Ford, P. Spong: Dialect change in resident killer whales: Implications for vocal learning and cultural transmission, *Anim. Behav.* **60**, 629–638 (2000)
- 20.132 B. McCowan, D. Reiss, C. Gubbins: Social familiarity influences whistle acoustic structure in adult female bottlenose dolphins (*Tursiops truncatus*), *Aqua. Mamm.* **24**, 27–40 (1998)
- 20.133 L.G. Grimes: Dialects and geographical variation in the song of the splendid sunbird *Nectarinia coccinigaster*, *Ibis* **116**, 314–329 (1974)
- 20.134 J.K.B. Ford: Vocal traditions among resident killer whales (*Orcinus orca*) in coastal waters of British Columbia, *Can. J. Zool.* **69**, 1454–1483 (1991)
- 20.135 F. Nottebohm: The song of the chingolo, *Zonotrichia capensis*, in Argentina: description and evaluation of a system of dialect, *Condor* **71**, 299–315 (1969)
- 20.136 J.K.B. Ford: Acoustic behaviour of resident killer whales (*Orcinus orca*) off Vancouver Island, British Columbia, *Can. J. Zool.* **67**, 727–745 (1989)
- 20.137 J.K.B. Ford, H.D. Fisher: Group-specific dialects of killer whales (*Orcinus orca*) in British Columbia. In: *Communication and Behavior of Whales. AAAS Sel Symp. 76. Boulder* (Westview Press, Boulder, CO 1983) pp. 129–161
- 20.138 J.K.B. Ford: *Call traditions and dialects of killer whales (Orcinus orca) in British Columbia*, Ph.D. Dissertation (Univ. British Columbia, Vancouver, BC 1984)
- 20.139 A.E. Bowles, W.G. Young, E.D. Asper: On ontogeny of stereotyped calling of a killer whale calf, *orcinus orca*, during her first year, *Rit Fiskideildar* **11**, 251–275 (1988)
- 20.140 H. Whitehead, S. Waters, L. Weilgart: Social organization in female sperm whales and their offspring: Constant companions and casual acquaintance, *Behav. Ecol. Sociobiol.* **29**, 385–389 (1991)
- 20.141 L. Weilgart, H. Whitehead: Group-Specific Dialects and Geographical Variation in Coda Repertoire in South Pacific Sperm Whale, *Behav. Ecol. Sociobiol.* **40**, 277–285 (1997)
- 20.142 C.W. Clark: Acoustic behavior of mysticete whales. In: *Sensory Abilities of Cetaceans*, ed. by J. Thomas, R. Kastelein (Plenum, New York 1990) pp. 571–583
- 20.143 A.E. Alling, E.M. Dorsey, J.C. Gordon: Blue whales (*Balaenoptera musculus*) off the northeast coast of Sri Lanka: distribution, feeding, and individual identification. In: *Cetaceans and Cetacean Research in the Indian Ocean Sanctuary*, Mar. Mammal Tech. Rep., Vol. 3, ed. by S. Leaderwood, G.P. Donovan (UNEP, New York, NY 1991) pp. 247–258
- 20.144 W.A. Watkins, P.L. Tyack, K.E. Moore, J.E. Bird: The 20-Hz signals of finback whales (*Balaenoptera physalus*), *J. Acoust. Soc. Am.* **82**, 1901–1912 (1987)
- 20.145 W.A. Watkins: The activities and underwater sounds of fin whales, *Sci. Rep. Whales Res. Inst.* **33**, 83–117 (1981)
- 20.146 R.S. Payne, S. Mcvay: Songs of humpback whales. Humpbacks emit sounds in long, predictable patterns ranging over frequencies audible to humans, *Science* **173**, 585–597 (1971)
- 20.147 D.A. Helweg, A.S. Frankel, J.R. Mobley Jr, L.M. Herman: Humpback whale song: our current understanding. In: *Sensory Abilities of Aquatic Mammals*, ed. by J.A. Thomas, R.A. Kastelein, Aya Supin (Plenum, New York 1992) pp. 459–483
- 20.148 B. Wursig, C. Clark: Behavior. In: *The Bowhead Whale*, Lawrence Soc. Mar. Mammal Spec. Publ., Vol. 2, ed. by J.J. Burns, J.J. Montague, C.J. Cowles (Allen, Lawrence 1993) pp. 157–199
- 20.149 W.C. Cummings, D.V. Holliday: Sounds and source levels from bowhead whales off Pt. Barrow, Alaska. *J. Acoust. Soc. Am.* **82**, 814–821 (1987)
- 20.150 W.C. Cummings, P.O. Thompson: Underwater Sounds from the Blue Whale, *Balaenoptera musculus*, *J. Acoust. Soc. Am.* **50**, 1193–1198 (1971)
- 20.151 P.L. Edds: Characteristics of the blue whale, *Balaenoptera musculus*, in St. Lawrence river, *J. Mamm.* **63**, 345–347 (1982)
- 20.152 M.A. McDonald, J.A. Hilderbrand, S.C. Webb: Blue and fin whales observed on a seafloor array in the northeast Pacific, *J. Acoust. Soc. Am.* **98**, 712–721 (1995)
- 20.153 W.C. Cummings, P.O. Thompson, S.J. Ha: Sounds from bryde's whale *Balaenoptera edeni*, and finback, *B. physalus*, whales in the gulf of California: Fishery bulletin, *Breviora Mus. Comp. Zool.* **84**, 359–370 (1986)
- 20.154 P.L. Edds, D.K. Odell, B.R. Tershy: Vocalization of a captive juvenile and free-ranging adult-calf pairs of bryde's whales, *Balaenoptera edeni*, *Mar. Mamm. Sci.* **9**, 269–284 (1993)
- 20.155 P.L. Edds: Characteristic of finback, *Balaenoptera physalus*, vocalization in the St. Lawrence estuary, *Bioacoustics* **1**, 131–149 (1988)

- 20.156 W.C. Cummings, P.O. Thompson: Characteristics and seasons of blue and finback whale sounds along the U.S. west coast as recorded at SOSUS stations, *J. Acoust. Soc. Am.* **95**, 2853 (1994)
- 20.157 M.E. Dalheim, D.H. Fisher, J.D. Schempp: Sound Production by the Grey Whale and Ambient Noise Levels in Laguna San Ignacio, Baja California Sur, Mexico. In: *The Grey Whale*, ed. by M. Jones, S. Swartz, S. Leatherwood (Academic Press, S.D. 1984) pp. 511–541
- 20.158 N.L. Crane: *Sound Production of Gray Whales, Eschrichtius tobustus Along Their Migration Route* (MS Thesis, San Francisco St. Univ., San Francisco, CA 1992)
- 20.159 W.C. Cummings, P.O. Thompson, R. Cook: Underwater sounds of migrating gray whales, *eschrichtius glaucus* (cope), *J. Acoust. Soc. Am.* **44**, 278–1281 (1968)
- 20.160 P.O. Thompson, W.C. Cummings, S.J. Ha: Sounds, Source Levels, and Associated Behavior of Humpback Whales, Southeast Alaska, *J. Acoust. Soc. Am.* **80**, 735–740 (1986)
- 20.161 R.S. Payne, K. Payne: Large scale changes over 19 years in songs of humpback whales in bermuda, *Z. Tierpsychol.* **68**, 89–114 (1985)
- 20.162 W.E. Schevill, W.A. Watkins: Intense low-frequency sounds from an antarctic minke whale, *Balaenoptera acutorostrata*, *Breviora Mus. Comp. Zool.*, 1–8 (1972)
- 20.163 H.E. Winn, P.J. Perkins: Distribution and sounds of the minke whale, with a review of mysticete sounds, *Cetology* **19**, 1–11 (1976)
- 20.164 W.C. Cummings, J.F. Fish, P.O. Thompson: Sound production and other behavior of southern right whales, *eubalena glacialis*, *Trans. San Diego Soc. Nat. Hist.* **17**, 1–13 (1972)
- 20.165 C.W. Clark: Acoustic Communication and Behavior of the Southern Right Whale. In: *Behavior and Communication of Whales*, ed. by R.S. Payne (Westview Press, Boulder, CO 1983) pp. 643–653
- 20.166 A.R. Knowlton, W.W. Clark, S.D. Kraus: Sounds Recorded in the Presence of Sei Whales, *Balaenoptera borealis*, in *Proc. 9th Bienn. Conf. Biol. Mar. Mamm.*, Chicago, IL, Dec. 1991, p. 40 (1991)
- 20.167 P.O. Thompson, L.T. Findlay, O. Vidal: Underwater sounds of blue whales, *Balaenoptera musculus*, in the Gulf of California, Mexico, *Mar. Mamm. Sci.* **12**, 288–293 (1987)