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Animal Acoustic Communication

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CHAPTER 6

Acoustic Communication Under the Sea

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1
Introduction

When one dives under the sea, it usually sounds relatively quiet. This is because the human ear is adapted to hear airborne sound. Our middle ear is designed to operate with air on both sides of the eardrum and it does not transmit sound very well when the outer ear canal is flooded with water. However, if one listens with a *hydrophone*, or underwater microphone, it is immediately apparent that the sea is full of sound. Some of this stems from physical processes, such as earthquakes or wind and waves. Humans and other animals also take advantage of unusual properties of underwater sound for communication and gathering information about their environment.

Of all the ways to transmit information over long distances through the sea, sound is the best. Light has the lowest attenuation through seawater of any frequency of electromagnetic radiation, yet even sunlight is reduced to about 1 % of its surface intensity at a depth of 100 m in clear water (Clarke and Denton 1962). The signals of most bioluminescent animals are unlikely to be visible beyond tens of meters. On the other hand, sound propagates so well underwater that a depth charge exploded off Australia can be heard in Bermuda (Shockley et al. 1982). These long ranges for underwater acoustic propagation differ strongly from most terrestrial environments in which one typically can see farther than one can hear or yell. There are also costs associated with acoustic displays for marine animals. Since underwater sound travels rapidly over great distances, acoustic signals can be intercepted by predators or animals other than the intended recipient. It is often advantageous to direct a display to one particular recipient in order to avoid this problem of interception. Limiting the audience of a display is often more difficult for acoustic displays than for visual or tactile ones.

Because animal sounds tend to carry farther underwater than one can see, marine biologists usually find it easier to hear a sound-producing animal than to see it. There are still loud sounds heard frequently in the ocean for which the source is completely unknown. One has the picturesque name of Wenz's boing. A Navy expert on ambient ocean noise named Wenz described a curious "boing" sound heard by sonar crews on submarines and from bottom mounted hydrophones in the North Pacific (Wenz 1964). Thompson and Friedl (1982) analyzed the seasonal occurrence of these "boings" over 2 years, and found that the source was heard in Hawaiian waters during the wintertime. Even though the boing has been recorded for over three decades, no one knows what kind of animal makes it. Besides the boing, the range of animal acoustic communication under the sea is rich. Biologists have reported that three groups of marine animals produce sounds underwater: crustaceans, fish, and marine mammals.

1.1
Invertebrates

Marine crustaceans can produce surprisingly loud impulse sounds. Spiny lobsters, *Panulirus* sp., produce a sound by moving a hard part of the body against a serrated area of their exoskeleton (Moulton 1957). This kind of sound production is called *stridulation*, and is similar to making sounds by moving one's fingernail along the teeth of a comb. Snapping shrimp of the genera *Crangon, Alpheus,* and *Synalpheus* make sounds by snapping the finger of a specially modified claw. Snapping shrimp often hold the finger cocked open in a retracted position, and the snapping sound is correlated with the rapid closure of the finger on the claw. The finger has a hard knob which fits into a socket in the claw. When the knob hits the socket, a jet of water flows out of a groove near the socket as a sharp snapping noise is produced. It is remarkable to think that an important source of ocean noise in coastal tropical and subtropical waters stems from millions of snapping sounds of these small crustaceans.

1.2
Fish

The common names of many fish, such as grunts, croakers, and drumfish, indicate that people have known for centuries that fish make sounds. However, fish sounds were only recorded with fidelity from the animals' natural environment after World War II, when hydrophones and portable recording devices became available to biologists. The growth of snorkeling and diving also provides opportunities for hearing the sounds of fishes. For example, if you have snorkeled in a coral reef, you may have heard the loud sounds produced by parrot fish as they bite into the coral. This sound is a necessary consequence of parrotfish feeding movements. It is not necessarily produced by the fish in order to communicate, but other fish nearby may attend to this reliable signal of feeding behavior. Many fish also have hard teeth in the pharynx and can produce stridulatory sounds using either these hard tissues or other hard tissues such as bone or spines of the dorsal or pectoral fins. Many different groups of fish also use an air-filled *swim bladder* to produce sounds. The swim bladder is located in the abdomen and initially evolved for buoyancy control in fish. Many species have evolved secondary uses of the bladder as an acoustic resonator. Swim bladder sounds are produced when contractions of specialized "sonic" muscles cause changes in the pressure and volume of the gas in the swim bladder. The vibrating surface of the resonating swim bladder acts as an efficient low frequency underwater loudspeaker (Tavolga 1964, pp. 195-211). The importance of the swim bladder has been demonstrated in experiments showing greatly reduced sound output in fish with damaged, deflated, or water-filled swim bladders (e.g., Tavolga 1962; Winn and Marshall 1963).

The lore of people who fish often includes caution about making noises that might disturb fish, but in the last century there has been considerable controversy among biologists about whether fish can hear. Along with his pioneering work on the dance language of honeybees, the German ethologist Karl von Frisch (1938) also performed an influential demonstration of fish hearing. Many earlier tests had shown that fish did not respond strongly to artificial noises. Frisch reasoned that the sounds simply might have had little significance to the fish. He trained a fish by whistling just before feeding it, and the fish soon would swim over at the sound of the whistle. By testing hearing abilities in fish after removal of various parts of the inner ear, von Frisch was able to determine which organs are responsible for hearing. Frisch had a genius for simple elegant experiments, and his work stands as an object lesson for students of biology that the more carefully thought out an experiment is, the simpler it often can be. Readers interested in a recent review on the role of underwater sound in fish behavior, including both sound production and hearing, can refer to Hawkins (1993). An elementary discussion of the hearing of fish and other animals is presented in Stebbins (1983). More detailed treatment of fish hearing can be found in Popper and Platt (1993). Extensive ethological study over the past several decades has shown that fish use sound for a broad variety of functions including reproductive advertisement displays, territorial defense, fighting assessment, and alarm (Myrberg 1981).

1.3
Marine Mammals

The sounds of marine mammals are such a part of our culture now that the reader may be surprised to learn that the first recordings identified from a marine mammal species were made in 1949. These were recordings of beluga whales, *Delphinapterus leucas*, reported by Schevill and Lawrence (1949, 1950) in the lower Saguenay River near the St. Lawrence estuary. Shortly afterwards, there was rapid growth in studies of how dolphins echolocate using high frequency click sounds and of field studies of low frequency sounds made by baleen whales. In the 1950s and 1960s, marine mammal bioacoustics was concerned primarily with identifying which species produced which sounds heard underwater. Much of this research were funded by naval research organizations because biological sources of noise can interfere with human use of sound in the sea. Readers interested in a historical perspective on marine bioacoustics during this time can refer to Schevill et al. (1962) and Tavolga (1964). Studies of echolocation in captive dolphins flourished particularly because of the obvious naval interest in exploring how dolphins achieve their remarkable echolocation abilities.

Controlled experiments on hearing and echolocation in dolphins have been critical for our understanding of auditory processes in cetaceans. For example, research on dolphins emphasizes that they can perform very rapid auditory processing for echolocation signals (Au 1993). Mammalian auditory systems appear to integrate energy over short intervals of time. This can be measured in experiments that vary either the duration of a signal or the interval of time between two clicks. When the interval is less than the integration time, the animal perceives as louder either the longer signal or the two-click signal. Experiments changing the duration of pure tones suggest dolphins have time constants on the order of 10 ms, close to that of humans, for frequencies from 500 to 10000 Hz. Bottlenose dolphins have also had the integration time tested using pairs of high frequency clicks and the interval measured is near 265μs. The 40-fold difference in integration time for these two kinds of signals suggests either that dolphins have a frequency-specific difference in the temporal characteristics of their peripheral hearing or that they have two different kinds of central auditory processing. Bullock and Ridgway (1972) found that different areas of the dolphin brain process these two kinds of signals. When they presented click sounds, there was a rapid response of an area of the midbrain called the *inferior colliculus*. Broad areas of the cortex of the brain showed slow responses to frequency modulated tonal sounds. This evidence supports the interpretation that differences in central processing may affect the integration time for these different stimuli.

There have been few studies relating acoustic communication to social behavior in marine animals compared with terrestrial ones. This stems in part from the agendas of funding agencies and in part because of difficulties observing marine animals in the wild. During the 1950s and 1960s, the communicative functions of vocalizations were only investigated in a few marine mammal species that could be studied in captivity, especially the bottlenose dolphin (*Tursiops truncatus*). More recent reviews of acoustic communication in marine animals (e.g., Myrberg 1981; Hawkins and Myrberg 1983) develop more of a communicative perspective, particularly for smaller animals that can easily be studied in relatively naturalistic captive settings. New methods have more recently opened up windows on the social behavior and communication of marine mammals (Costa 1993). For example, the United States Navy has recently made networks of bottom-mounted hydrophone arrays available to biologists, even though these were closely guarded military secrets during the Cold War. These arrays allow biologists to track vocalizing whales hundreds of kilometers away. The increased power and reduced size of electronics have also allowed the development of new devices that can be attached directly to wild animals. For example, new tagging technology has allowed biologists to record the acoustic stimuli an animal hears, as well as its vocal and physiological responses, even if the animal is 1000 m deep and hundreds of kilometers away from where it was tagged. Bothlong-range acoustic detections of whale vocalizations and the ability to tag highly mobile animals have radically expanded the effective ranges of our ability to study marine mammal communication. This chapter will focus on some of these new techniques and results. Since the author's own expertise covers marine mammals, and since several earlier chapters on marine bioacoustics emphasize fish (e.g., Hawkins and Myrberg 1983), this chapter will emphasize examples from marine mammals.

1.4
Organization of This Chapter

The basic goal of this chapter is to present acoustic communication by marine organisms in the context of ocean acoustics. The author first discusses some basic features of ocean acoustics and propagation of sound in the sea, and uses this information to discuss long-range communication by whales. The equation used to estimate the operating range of a sonar is applied to dolphin sonar. Hearing and the use of underwater sounds in communication are then discussed for invertebrates, fish, and marine mammals, with special emphasis on agonistic signals, reproductive advertisement displays, and recognition signals. Several issues of particular importance to marine mammals are then detailed, including vocal learning among marine mammals, how vocal learning affects communication, and promising new bioacoustic techniques. The first paragraph of Section 1.3 mentions that one early impetus for studying the sounds of marine organisms came from potential interference with human activities. As we learn how much marine animals have come to rely upon sound for their own critical activities, and as endangered marine mammal species have received increased protection, there has been increased concern about the impact of anthropogenic noise on marine animals (Green et al. 1994). The chapter closes with a discussion of this issue.

2
Elementary Acoustics

When a loudspeaker is turned on, the cone moves in and out, and it causes molecules in the surrounding air to move. As the nearby molecules move out, they cause an increase in pressure that induces an outward motion of neighboring particles. This *particle motion* induced by a moving or vibrating source can propagate through any compressible medium including gases such as air or liquids such as seawater. Sound induces motion in any elastic objects in the medium. In order to be sensed by a nervous system or electronic gear, this mechanical energy must be converted into electrical energy. In animals, this is typically generated when motion of the external medium bends hair-like *cilia* on specialized sensory cells. This bending of the cilia modifies the voltage difference between the inside and the outside of the sensory cell. This voltage difference in turn can modify the rate of action potentials produced by the cell. Engineers, on the other hand, typically convert mechanical into electrical energy using crystals or ceramics that have the *piezoelectric* property, i.e., they generate a voltage difference when subjected to pressure forces. Much of the advancement in marine bioacoustics of the past few decades stems from the ready availability of small efficient underwater microphones, or hydrophones, using these piezoelectric ceramics. These ceramic sensors have a high impedance, so if one needs a cable more than 10 m or so long, one must buffer the signal to a lower impedance with a preamplifier. The preamplifier and ceramic sensor are typically potted in a waterproof compound with the same density and speed of sound as water. The entire assembly can be on the order of 1 cm in diameter, small enough to attach to a large animal or to install in a small aquarium. If one needs to quantify actual pressure levels of sound, one can either purchase calibrated hydrophones, or calibrate them oneself with respect to a calibrated reference hydrophone.

2.1
Frequency and Wavelength

A sound that we perceive as a pure tone has a sinusoidal pattern of pressure fluctuations. The *frequency* of these pressure fluctuations is measured in cycles per second. The modern name for this unit of frequency is the Hertz (Hz), and just as 1000 meters are called a kilometer, 1000 Hertz are called a kiloHertz (kHz). The *wavelength* of this tonal sound is the distance from one measurement of the maximum pressure to the next maximum. Sound passes through a homogeneous medium with a constant speed, c. The speed of sound in water is approximately 1500 m/s, roughly five times the value in air, 340 m/s. The speed of sound c relates the frequency f to the wavelength λ by the following formula: $c = \lambda f$. Thus the wavelength of an underwater sound of frequency f has about five times the wavelength of the same frequency in air. Imagine the significance of this difference for the sound localization abilities described by Pye and Langbauer (this Volume). An animal that locates a sound of a particular frequency by measuring the delays in arrival time of a signal at both ears would need five times the separation between ears underwater to achieve the same effective size as in air. Not all sounds are tonal. Sounds that have energy in a range of frequencies, say in the frequency range between 200 and 300 Hz, would be described as having a *bandwidth* of 100 Hz.

2.2
Sound Pressure Level and the Decibel

It is seldom possible to follow acoustic measurements without understanding the unusual measurement scale adopted by acousticians. This scale, called the *decibel* (dB), may be facetiously thought of as a way to limit acoustic calculations to adding and subtracting integers from 1 to 200 or so. Physicists are used to complex mathematical manipulations of variables in a small set of basic units, even if the numbers vary from $10^{-\text{lots}}$ to $10^{+\text{even more}}$. By comparison, an acoustic engineer creates a complex scale to keep later calculations simple. Most acoustic calculations involve multiplication, so the acoustic engineer performs a logarithmic transformation to convert the multiplication operation to addition — remember that the $\log(A \times B) = \log(A) + \log(B)$. This logarithmic transformation is called the *bel* scale, in honor of Alexander Graham Bell. However, if one wants to round off the numbers to integers, this logarithmic transformation limits precision too much. To get around this, the acoustic engineer multiplies the logarithm by 10 to convert the bel to the decibel or dB.

Sound transmits energy via the propagating pressure fluctuations. Sound *intensity* is the amount of energy per unit time (power) flowing through a unit of area. The intensity of a sound equals the acoustic pressure squared divided by a proportionality factor which is specific for each medium. This factor is called the specific acoustic resistance of the medium, and equals the density of the medium, ρ, times the speed of sound, c.

$$Intensity = \frac{Pressure^2}{\rho c} \tag{1}$$

Seawater has a higher acoustic resistance than air. The ratio of the acoustic resistance of seawater divided by that of air is about 3571 or in decibel terms = 10 log (3571) = 35.5 dB. For a given sound pressure, the intensity of this sound in water would be 35.5 dB less than the intensity for the same pressure level in air. If I and I_{ref} are two intensities, their difference in dB is calculated as follows:

$$Intensity = 10\ log \frac{I}{I_{ref}}\ dB \tag{2}$$

In order that intensity levels and pressure levels be comparable in dB, the sound pressure level (SPL) is defined as follows:

$$SPL = 20\ log \frac{P}{P_{ref}}\ dB \tag{3}$$

This maintains the appropriate proportionality of intensity and pressure (if $I \propto P^2$ then $\log I \propto 2 \log P$) for sounds in the same medium. As an example, take a sound measured to be ten times the pressure reference. This would be 20 dB by the definition of SPL in Eq.(3). Since intensity is proportional to pressure squared, the intensity of this sound would be 10^2 or 100 times the intensity of the reference. This would still be 20 dB re the reference intensity, by the definition of intensity in Eq.(2).

The primary definition of the decibel is as a ratio of intensities. The decibel always compares a pressure or intensity to a reference unit. Both intensities and pressures are referred to a unit of pressure, 1 μPa, in a form of shorthand. When an *intensity* is referred to pressure of 1 μPa, it really means referred to the intensity of a continuous sound of pressure equal to 1 μPa. Acousticians seldom measure intensity directly though, because microphones and hydrophones measure pressure. There have been a plethora of references used over the years (see Urick 1983, p. 14-15). One standard for airborne acoustics was the lowest pressure level humans could nominally hear, 0.000204 dyne/cm^2. The current standard reference is less anthropocentric and more closely related to standard units. In SI units, pressure is measured in newtons per meter squared, or Pascals (Pa). The standard reference pressure for underwater sound is 10^{-6} Pa or 1 μPa. This equals 10^{-5} dyne/cm^2 and is -26 dB with respect to the airborne sound standard. In order to convert a sound level referred to the airborne standard of 0.000204 dyne/cm^2 to the 1 μPa standard, add 26 dB. Another earlier reference pressure is the μ*bar*, which equals 1 dyne/cm^2. If one μPa equals 10^{-5} dyne/cm^2 then it is 20 log (10^{-5}) = -100 with respect to 1 μbar. Thus, if there is a reference to a sound pressure level with respect to 1 μbar, just add 100 to get the equivalent level with respect to 1 μPa.

3

Propagation of Sound in the Sea

The propagation of sound energy is described mathematically by the *wave equation.* Two solutions are typically used to model the propagation of underwater sound: *normal mode theory* and *ray theory.* In this section, the author will fall back upon more qualitative descriptions of familiar ray phenomena such as refraction. The reader interested in a more quantitative introductory treatment of underwater sound should refer to Clay and Medwin (1977). The three major factors affecting the speed of sound in seawater are temperature, salinity, and pressure. Water is warmed near the surface of the ocean in most locations and seasons. This leads to an increase in the speed of sound as one approaches the sea surface. Below this warmed layer there is less change of temperature with depth, and sound speed is dominated by increasing pressure. At greater depths, the sound speed increases with increasing pressure (Ewing and Worzel 1948).

Like light passing through a lens, sound rays are refracted when they pass from a medium with one sound speed c_1 to a medium with a different sound speed c_2. The angles of these sound rays are measured between the rays and a line normal to the interface between the two media (Figure 1). The change in angle of such a ray at a sound speed boundary is defined by *Snell's law*:

$$\frac{sin(\theta_1)}{c_1} = \frac{sin(\theta_2)}{c_2} \tag{4}$$

If one visualizes a sound front emanating from a source at a depth corresponding to the minimum in sound speed, one can see that a horizontal ray would continue horizontally as long as it remained in a zone of constant *c*. However, rays with vertical components would start refracting back towards the axis of minimum speed as they traveled up or down into areas of faster *c*. A simple numerical example may illustrate this. Suppose a ray launches in water with a sound speed of c_1 with an angle of 45° with respect to vertical in the upward direction and encounters a transition to a horizontal

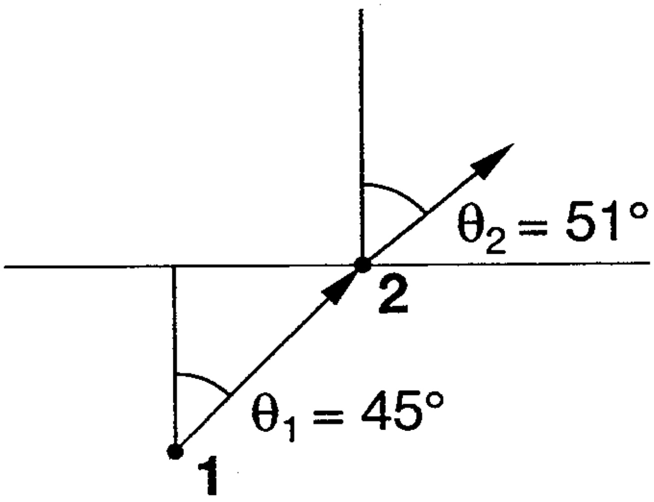

Fig. 1. Refraction using Snell's law. A sound ray starts at point 1 in a medium with a speed of sound c_1 and with an angle of θ_1. At point 2, it encounters a horizontal layer above which the sound speed, c_2, is 1.1 times faster. This change in the speed of sound from c_1 to c_2 causes the sound to refract to an angle of θ_2. Both angles are measured with respect to the vertical

layer of water in which the sound speed, c_2, is 10 % faster (Figure 1). In this case, where $c_2=1.1 \times c_1$, the new ray angle $\theta_2=\arcsin[1.1(\sin 45°)]=51°$, an angle closer to horizontal. The upward traveling ray thus deflects downward as it travels into water where the speed of sound is faster. A ray traveling downward from the depth of the minimum sound speed would similarly refract back towards that depth. Refraction in the deep ocean thus creates a channel in which sound energy concentrates at depth.

3.1
Transmission Loss

Imagine a source producing a sound impulse in a uniform unbounded space. At the moment the sound is produced, all of the sound energy will be centered at the source. After time *t* when the sound front has traveled out to range *r*, the energy will be distributed over a sphere of area = $4\pi r^2$. Just as for gravity, the intensity of the signal at any one point decreases as the square of the range. This is called the *inverse-square law* for gravity and *spherical spreading* for underwater acoustics. This loss of intensity as one moves farther from the source is called *transmission loss* (TL). In the dB nomenclature of acousticians, this transmission loss is calculated as follows:

Spherical spreading:
$$TL = 10\ log\frac{I}{I_{ref}} = 10 log\frac{4\pi r^2}{4\pi r_{ref}^2} = 20\ log\frac{r}{r_{ref}} \qquad (5)$$

The typical reference range is 1 m yielding TL=20 log r. Sound propagates by spherical spreading when the sound energy is free to spread in all directions. This occurs until the sound encounters a boundary with different acoustic properties such as the sea surface or ocean floor. As mentioned in Section 3, sound may also encounter areas of water with different acoustic properties within the ocean which can cause refraction. When one is far from a sound source compared with the ocean depth, the sound energy may be concentrated by refraction in the deep ocean sound channel. This sound can be thought of as spreading in a plane, to a first approximation. In this case, sound energy at time *t* would be distributed over a circle of area = $2\pi r$. Since the sound energy is not really restricted to a plane, but more like to a short wide cylinder, it is known as cylindrical spreading and follows a TL = 10 log *r* dB.

Cylindrical spreading:
$$TL = 10\ log\frac{I}{I_{ref}} = 10 log\frac{2\pi r}{2\pi r_{ref}} = 10\ log\frac{r}{r_{ref}} \qquad (6)$$

If sound interacts with the sea surface or ocean bottom, then there is some loss of acoustic energy to these interfaces. In these intermediate conditions and transmission in coastal waters, the transmission loss is often somewhere between 10 and 20 log *r*.

3.2
Absorption

Sound spreading is a dilution factor and is not a true loss of sound energy. *Absorption* on the other hand is conversion of acoustic energy to heat. The attenuation of sound due to absorption is a constant number of dB per unit distance, but this constant is dependent upon signal frequency, as the following approximate figures in Table 1 indicate.

Table 1. Absorption coefficient for 14°C seawater at sea level (approximated from Figure 3.3.1 in Clay Medwin 1977, pp. 100-101)

Frequency	Absorption coefficient (dB/m)
100 Hz	10^{-6}
1 kHz	10^{-4}
10 kHz	10^{-3}
40 kHz	10^{-2}
300 kHz	10^{-1}
2 MHz	1

While absorption yields trivial effects at frequencies below 100 Hz, it can significantly limit the range of higher frequencies, particularly above 40 kHz or so, where the loss is more than 1 dB/100 m.

3.3
Sonar Equation

During World War II, acoustic engineers worked out equations to predict the performance of different sonar systems. These *sonar equations* are still used to predict the detection range of an underwater sound (Urick 1983). These equations are convenient for back-of-the-envelope-type calculations, but predict only in an average sense. A simple form of the *passive sonar equation* is:

$$RL(dB) = SL(dB) - TL(dB) \tag{7}$$

We have already seen the last term on the right side of the equation, *transmission loss* (Sect. 3.1). Source level is the sound intensity measured in decibels with respect to a reference distance, usually 1 m. Transmission loss is the difference between the source level at the reference distance and the intensity predicted for the range of the receiver. RL is the *received level* of sound at the receiving hydrophone, measured in dB. The likelihood of detecting a signal does not just depend upon the received level but also depends upon the external environmental noise as well as any internal noise in the receiver. It is the ratio of signal to noise that is used to calculate the probability of detection. Using the logarithmic terms of the dB scale, this *signal to noise ratio* (SNR) is expressed as a subtraction:

$$SNR(dB) = RL(dB) - NL(dB) \tag{8}$$

where NL is the *noise level*.

While the signal to noise ratio is a simple concept, there are some complications that may improve performance. If a directional receiver is able to listen only in the direction of an incoming signal, then it will boost the strength of both signal and noise in this direction at the expense of reception from other directions. If the noise comes from all directions and the signal only from one direction, then the directional receiver increases the strength of the signal compared with the noise. Receivers can also be designed to match the frequency and time characteristics of the sonar signal. A receiver with a bandwidth well tuned to the signal bandwidth buys the equivalent of extra gain from reduction in noise outside the frequency range of the signal. Noise is often described in terms of a *spectrum level*, which is the noise level in a frequency band that is 1 Hz wide. The intensity of sound across a broader band of frequencies is called the *band level*. If the noise has the same energy at different frequencies across a frequency band, then the noise level within a frequency band *W* Hz wide will be:

$$Band\ \ level = spectrum\ level + 10\ log\ W \tag{9}$$

If the receiver integrates signals over some period of time, then it is also beneficial for the integration time to be well matched to the duration of the sonar signal. If a receiver has an integration time, t_{int}, that is longer than a short pulse, t_{pulse}, then the effective source level of the sound, SL', will be reduced by the following amount:

$$SL'(dB) = SL(dB) + 10 log \frac{t_{pulse}}{t_{int}} \tag{10}$$

3.3.1
Long-Range Sound Transmission by Whales

We now have enough information to understand how some whale sounds are adapted for long-distance communication. Finback whales, *Balaenoptera physalus*, produce pulses with energy in a range roughly between 15 and 30 Hz (Watkins et al. 1987), near the lowest frequencies that humans can hear. Absorption is negligible at these frequencies. These finback pulses qualify as infrasonic signals as discussed by Pye and Langbauer (this Volume). Each pulse lasts on the order of 1 s and contains 20 cycles. The source level of the pulses ranges from about 170 to 180 dB re 1 μPa (Patterson and Hamilton 1964). Particularly during the breeding season, finbacks produce series of pulses in a regularly repeating pattern in bouts that may last more than 1 day (Watkins et al. 1987). These sounds were first detected by geologists who were monitoring hydrophones installed on the sea floor in order to study submarine earthquakes (Patterson and Hamilton 1964). Figure 2 is a record from a seismographic drum recorder made on 18 November 1978 which shows a regular series of these pulses.

Figure 3 from Spiesberger and Fristrup (1990) shows the ray paths predicted for a sound pulse produced by a finback whale at 35 m depth, reaching a receiver at 500 m depth, 400 km away. These paths are predicted for a sound speed profile typical of temperate or tropical seas. The computer model used to predict the propagation of this sound suggests that a 186 dB finback signal produced at 35 m depth in the deep ocean

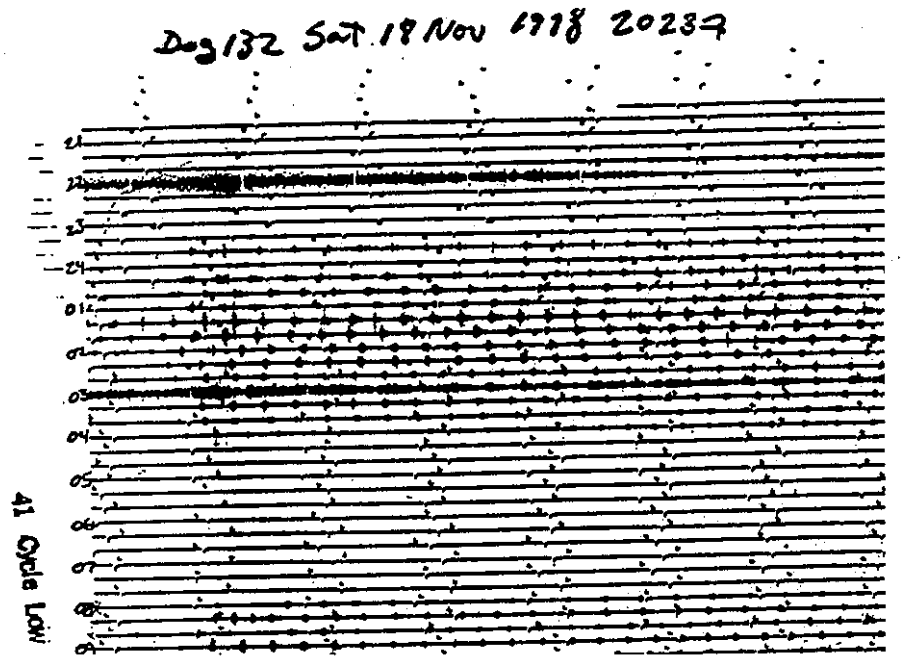

Fig. 2. Seismographic drum recording from a hydrophone off Bermuda. The hydrophone signal was filtered to cut out energy above 41 Hz. This filtered signal then drives a pen which records the waveform on the paper. Regular marks every minute mark timing of the signal, with each line taking 20 min. In order to expand the record, the *right-hand side* has been cut off, so only 7 out of each 20 min are shown. The signal starts at 202307, or 20:23 h. Around 22:00 h a ship passes by, marked by steadily increasing and then decreasing energy. Between 23:00 h and 24:00 h, a finback whale starts producing its regular pulses, which continue through the passage of another ship near 03:00 h. The whale finally stops sometime near 04:00 h

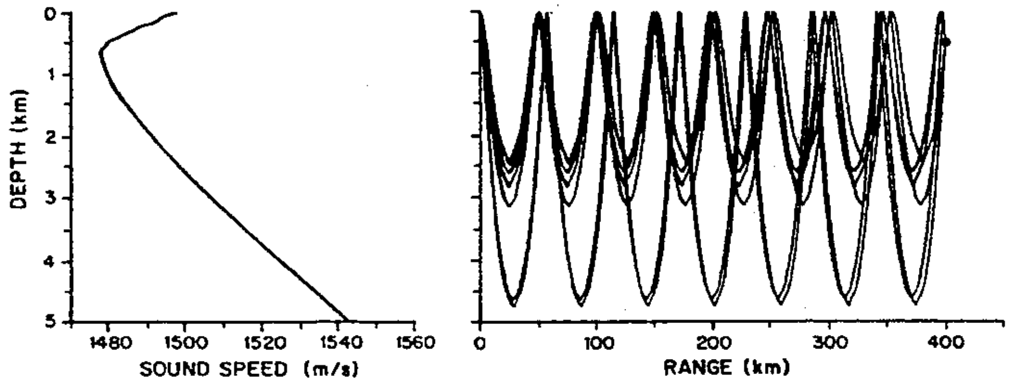

Fig.3. *Left* Typical profile of sound speed vs. depth for temperate or tropical seas. This particular profile was taken in the northeast Pacific near 31°N and 157°W. *Right* calculated ray paths for a 20-Hz finback pulse produced at range 0 and a depth of 35 m. Rays detected at a receiver 500 m deep and 400 km away are shown. The ray paths illustrate the general patterns of propagation of this kind of signal in deep temperate or tropical seas. Reprinted with permission from Spiesberger and Fristrup (1990) © The University of Chicago Press

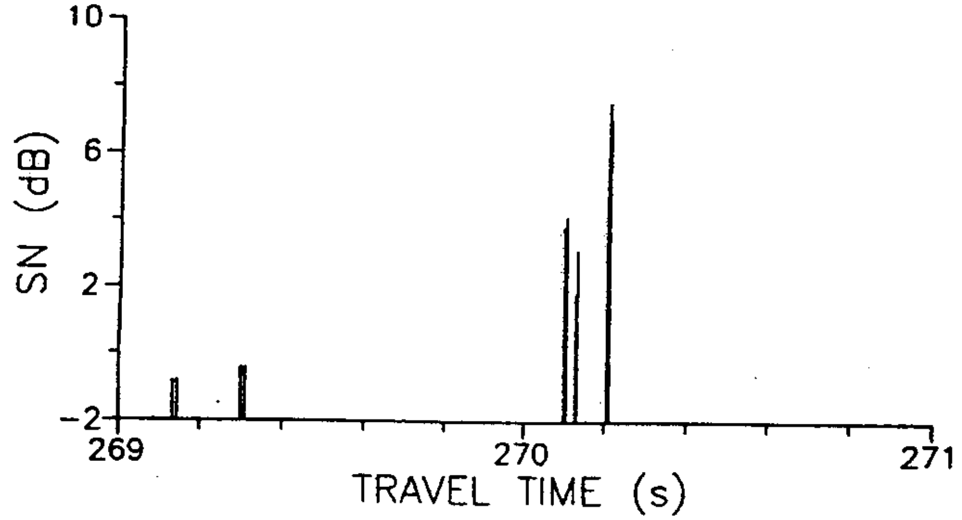

Fig. 4. Travel times and signal to noise ratios for the different acoustic ray paths shown in Fig. 3. Signal-to-noise ratios are calculated for a receiver which correlates a stored version of the outgoing pulse against the incoming signals. Reprinted with permission from Spiesberger and Fristrup (1990) © The University of Chicago Press

would be easily detectable out to a range of 400 km for a receiver at a depth of 500 m. The separate arrivals of the different rays arriving at this receiver 400 km away are illustrated in Figure 4, also from Spiesberger and Fristrup (1990). Many of the ray arrivals are well above (by 4 — 6 dB) typical ambient noise levels. As can be seen, the single pulse made by the whale is greatly modified by the channel. The separate rays from one pulse will arrive at different sound levels over a period of approximately 1 s. Since the pulse itself lasts 1 s, these different arrivals will superimpose, yielding a complex pattern. The simple acoustic structure of the finback calls may simplify recognition of these signals even when different arrivals are superimposed. The high rate of repetition and redundancy of these simple pulses in a well-defined sequence is also useful for communication in a noisy channel.

Refraction in the deep ocean causes most acoustic rays to center around the depth of minimum sound speed, *c*, which is called the axis of the sound channel. This channel is around 1 km deep in tropical or temperate oceans. If sound energy concentrates at depths near 1000 meters, then this would be a good depth for receiving the signals. However, finback whales are not known to dive deeper than a few hundred meters. The acoustic rays converge near the surface every 52 km, in what is known as a convergence zone (Figure 3). While baleen whales are not known to dive near the axis of the deep sound channel, a whale swimming through a convergence zone might experience an increase in sound level of 10-20 dB, perhaps even within a few tens of meters (Urick 1983). Other environments have very different propagation conditions. Arctic propagation under ice cover is dominated by upward refraction and downward reflection off the ice. This causes sound energy to concentrate in shallower waters and favors the frequency band from 15 to 30 Hz. Even away from ice cover, polar waters are subject to less surface warming, and this causes the sound velocity minimum to occur much closer to the surface in polar seas. Baleen whales in polar waters could dive nearer the axis of sound spreading than in temperate or tropical deep ocean.

A correlation of these 20 Hz series with the finback reproductive season suggests that they may function as reproductive advertisement displays (Watkins et al. 1987). Finback whales disperse into tropical oceans during the mating season, unlike other species such as humpback and gray whales which are thought to congregate in well-defined breeding grounds. The functional importance of a signal adapted to long-range communication is obvious for animals that disperse over ocean basins for breeding. However, even though biologists can hear finback pulses at ranges of hundreds of kilometers by listening at appropriate depths, the effective range of these signals for finbacks themselves is not known. Until very recently, marine bioacousticians have had few methods which would allow us to detect whether a whale was responding to the calls of a whale more than several kilometers away. The US Navy hydrophone arrays mentioned in Section 1.3 can provide such data, but first let us make a rough estimate of the range of detection for finback pulses.

3.3.2

Using the Sonar Equation to Estimate the Range of Detection for Finback Pulses

The threshold of detection for a signal is often considered to occur when the signal level equals the background level of masking noise. In order to compare these two, it is necessary to establish the appropriate frequency band for comparing signal and noise. Many finback pulses have maximum energy in a frequency range from about 18 to 23 Hz. This 5 Hz bandwidth comprises about one-third of the octave from 15 to 30 Hz. Research on hearing in mammals suggests that for noise to mask a tonal sound effectively, it must be within approximately one-third octave of the frequency of the signal (for a review of this issue applied to marine mammals, see Richardson et al. 1995). Thus, both the frequency range of the finback pulse and the bandwidth of mammalian hearing suggest measuring both signal and noise in the 18 – 23 Hz one-third octave interval in the 15 – 30 Hz octave band. The passive sonar equation allows us to make a rough estimate of the average intensity of a signal as a function of range. In the case of the finback pulses we need not concern ourselves with absorption loss, since even at 100 Hz the loss over 4×10^5 m is <1 dB. On the other hand if we were analyzing a 10 kHz signal, absorption would be $4 \times 10^5 \text{ m} \times 10^{-3} \text{ dB/m} = 400$ dB, well in excess of the spreading loss. Suppose we assume spherical spreading from the reference distance of 1 m to the depth of 5000 m and cylindrical spreading from 5 km to 400 km, then the calculation of transmission loss is as shown in Table 2.

Spiesberger and Fristrup (1990) used a source level of 186 dB for their finback pulse.

Table 2. Calculation of transmission loss (TL) using sherical spreading (20 log *r*) to 5000 m and cylindrical spreading (10 log *r*) from 5 to 400 km

Δ Range	TL (dB)
20 log 5000/1m	74
10 log 400/5km	19
Attenuation	<<1
Total	93

Table 3. Calculations in decibels of signal to noise ratio (SNR) from modification of the passive sonar-equation
[Eq. (7)]: RL=SL - TL, and,
[Eq. (8)]: SNR = RL - NL

SL	186
- TL	-93
= RL	93
-NL (18-23 Hz)	-77
=SNR	16

If we use the transmission loss estimated in Table 2, then the received level would be RL = SL-TL = 186 - 93 = 93 dB (Table 3). Now let us estimate the signal to noise ratio for the finback signal. Spiesberger and Fristrup (1990) estimate the noise level in the 18—23 Hz third octave band to be approximately 77 dB in the area they selected. This would indicate that the signal to noise ratio would be SNR = RL - NL = 93 - 77 = 16 dB louder than the ambient noise level (Table 3).

This result is 8 dB or more higher than the signal to noise ratio shown in Figure 4, which is predicted from ray theory. This kind of difference is not exceptional. The sonar equations give results that are highly averaged over time, range, and depth. They are best used for initial general tests of potential operating range. More detailed analytical methods are available, particularly when one knows more about a particular application. Ray theory is often used for deep water in the open ocean. Mode theory is more appropriate for propagation in water that is shallow with respect to the wavelengths of sound being used. There are also computer programs which can simplify solutions of equations for wave propagation. The reader interested in reviews of these more complex analyses can refer to Clay and Medwin (1977) for ray and mode theories and Tappert (1977) for parabolic equation solutions to the wave equation.

3.3.3
Echolocating Dolphins

Dolphins have highly developed abilities for echolocation. They can detect distant objects acoustically by producing loud clicks and then listening for echoes. These abilities are truly remarkable. For example, trained bottlenose dolphins can detect the presence of a 2.54-cm solid steel sphere at 72 m, nearly a football field away (Murchison 1980). They can discriminate targets that are identical in terms of shape and differing only in composition (e.g., Kamminga and van der Ree 1976). Most of these echolocation sounds are pulses of short duration and high frequency. By minimizing duration, dolphins are able to minimize the chance that the echo from the start of the signal will arrive before the signal has ended. Depending upon how dolphins process echoes, this can also improve the precision of estimating the distance to the target and facilitates discrimination of multiple echoes.

The optimal frequency of a sound used for echolocation depends upon the expected target size. Absorption imposes a significant penalty for higher frequencies, but small targets can best be detected by short wavelength λ or high frequency signals. In the last century, Lord Rayleigh solved the frequency dependence of sound scattering from small rigid spherical targets of radius r; this is called *Rayleigh scattering* (Rayleigh 1945). A spherical target reflects maximum energy when the wavelength of the sound impinging on it equals the circumference of the sphere, or $\lambda=2\pi r$. There is a sharp drop off of echo strength from signals with wavelength $\lambda > 2\pi r$. If one refers to Section 2.1 one sees that $\lambda = c/f$. If we equate the two λ terms we get $c/f = 2\pi r$. We can rearrange these to derive the relationship $f = c/2\pi r$ to calculate the optimal frequency for reflecting sound energy off a spherical target of radius r. Higher frequencies than this would still be effective sonar signals, but frequencies below f would show a sharp decrease in effectiveness with decreasing frequency.

Except for the dolphins trained to tell acousticians how they echolocate, most dolphins are presumably less interested in rigid spheres as targets than in fish, squid, sharks, conspecifics, and large obstacles. Living organisms have properties that differ from rigid spheres (Stanton et al. 1995), but let us use the formula for rigid spheres for first approximations. If a dolphin needs to use echolocation to detect targets about 1 cm in size or with a "radius" of 0.5 cm, it would do well to use a frequency $f = c/2\pi r = 1500/(2\pi \times 0.005)$ = near 50 kHz. This is in fact on the low end of the typical frequency range of dolphin echolocation clicks (Au 1993). The echolocation signals of dolphins include energy up to about 150 kHz, which would be well suited to detecting spherical targets with radii as small as 1.5 mm. For larger targets, these higher frequencies could improve the resolving power of dolphin echolocation for features about 1 mm in size. The hearing of toothed whales is also tuned to be most sensitive at these high frequencies. Figure 5 shows audiograms for two of the toothed whale species which have been kept in captivity under

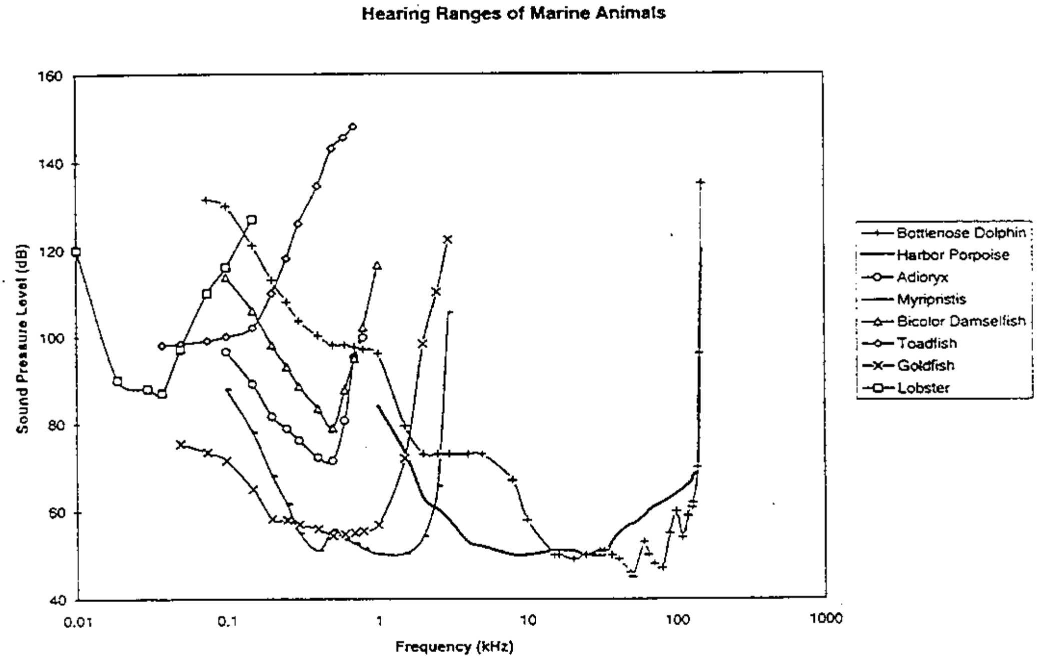

Fig. 5. Audiograms of selected marine animal species. The lines on the right indicate the audiogram of the bottlenose dolphin, *Tursiops truncatus*, indicated by "+"*Symbols*, (Johnson 1966) and of the harbor porpoise, *Phocoena phocoena*, indicated by the *thick black line* (Andersen 1970). The lines centering in the 100-1000 Hz range are of fish — *Adioryx* indicated by the circle symbols and *Myripristis* indicated by the *small filled black rectangles* (Coombs and Popper 1979); bicolor damselfish, *Pomacentrus partitus*, indicated by *the triangle symbols* (Myrberg and Spires 1980); toadfish, *Opsanus tau*, indicated by the diamond symbols (Fish and Offut 1972); and Goldfish, *Carassius auratus*, indicated by the "x" *symbols* (Jacobs and Tavolga 1967). The line far left with the *square symbols* indicates audiogram of the American lobster, *Homarus americanus*, (Offut 1970). Sound pressure levels are in decibels re 1μPa

conditions where they could be trained in order to test their hearing sensitivity — the bottlenose dolphin (*Tursiops truncatus*) and harbor porpoise (*Phocoena phocoena*).

Echolocation has only been studied in a small minority of dolphins and toothed whales, a taxonomic group called the odontocete cetaceans. There is considerable variety in clicks recorded from these animals. Figure 6 shows two examples of odontocete echolocation pulses: one from the bottlenose dolphin (*Tursiops truncatus*) and one from the harbor porpoise (*Phocoena phocoena*). The *Tursiops* pulse has a very sharp rise time on the order of tens of microseconds, and a very high maximum peak to peak sound pressure level, >220 dB re 1 μPa SPL at 1 m. The pulses of bottlenose dolphins from open waters are typically reported to have energy in a rather broad range of frequencies from about 100 to 130 kHz (Au 1993). The one illustrated in Figure 6 has a peak frequency of 117 kHz and a bandwidth of 37 kHz. The harbor porpoise has a high frequency component to its echolocation pulse tuned around a center frequency of 120–150 kHz with sound pressure levels of around 150–160 dB (Møhl and Anderson 1973; Kamminga and Wiersma 1981, Goodson et al. 1995). These have a longer duration (hundreds vs. tens of microseconds) and narrower bandwidth (10–15 kHz vs. 30–60 kHz) than typical clicks from bottlenose dolphins (Au 1993). Odontocetes have some ability to vary their echolocation pulses. For example, when the echolocation clicks of a beluga whale, *Delphinapterus leucas*, were tested in San Diego, the clicks had peak energy in the frequency band 40–60 kHz (Au et al. 1985). When the beluga was moved to Kaneohe Bay, Hawaii, where there is a high level of noise in these frequencies, it shifted its clicks to have peak energy mostly above 100 kHz.

If a sound transmitter can direct its output in the direction of the target, it buys the

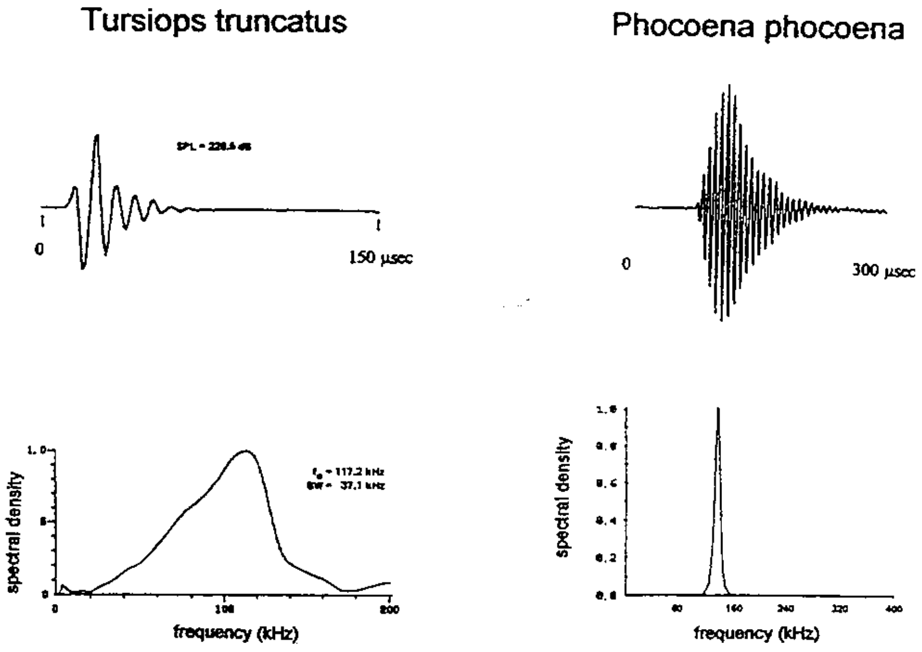

Fig.6. Waveform (*top*) and spectra (*bottom*) of clicks from bottlenose dolphins, *Tursiops truncatus*, (*left*) and harbor porpoise, *Phocoena phocoena* (*right*). The bottlenose dolphin diagrams show an average from an entire click train adapted from Au (1980). The harbor porpoise diagrams, adapted from Kamminga (1988), show a single click from a young animal

equivalent of a higher source level. In general, for a sound source of a given size, the higher the transmitting frequency, the more directional one can make the signal. This benefit of directional signals may be another reason why dolphins have evolved such high frequency echolocation signals. The clicks of bottlenose dolphins are highly directional, losing half their energy (3 dB) when just 10° off the main axis. Figure 7 shows the vertical beam pattern of *Tursiops* echolocation clicks (Au et al. 1978). The source levels indicated for *Tursiops* clicks were recorded in the center of the beam, so they take this gain into account. The transmit beam pattern of odontocete clicks is not necessarily fixed. The clicks of a false killer whale, *Pseudorca crassidens*, were recorded by Au et al. (1995) while the whale discriminated artificial targets. The whale produced four different kinds of click signals, each one with a different beam pattern. There was also quite a strong relationship between the source level of a click and its center frequency, with louder clicks having higher center frequencies. While the acoustic structure of odontocete clicks has been well documented as animals echolocate on artificial targets, we know very little about how clicks may vary when these animals are working on different echolocation tasks in the wild. Future research may find even more variability in the clicks used by dolphins to solve the problems in the natural environment for which echolocation evolved.

As was discussed when SNR was introduced, the ability to hear better along the target axis can improve the performance of a sonar system by reducing signals and noise from other directions. Dolphins have directional hearing that is well correlated with the beam pattern of their echolocation clicks (Au and Moore 1984). If NL is the noise level measured by an omnidirectional hydrophone, then the receiving directivity (DI) increases the signal to noise ratio (SNR) by DI if the noise is omnidirectional and the signal is

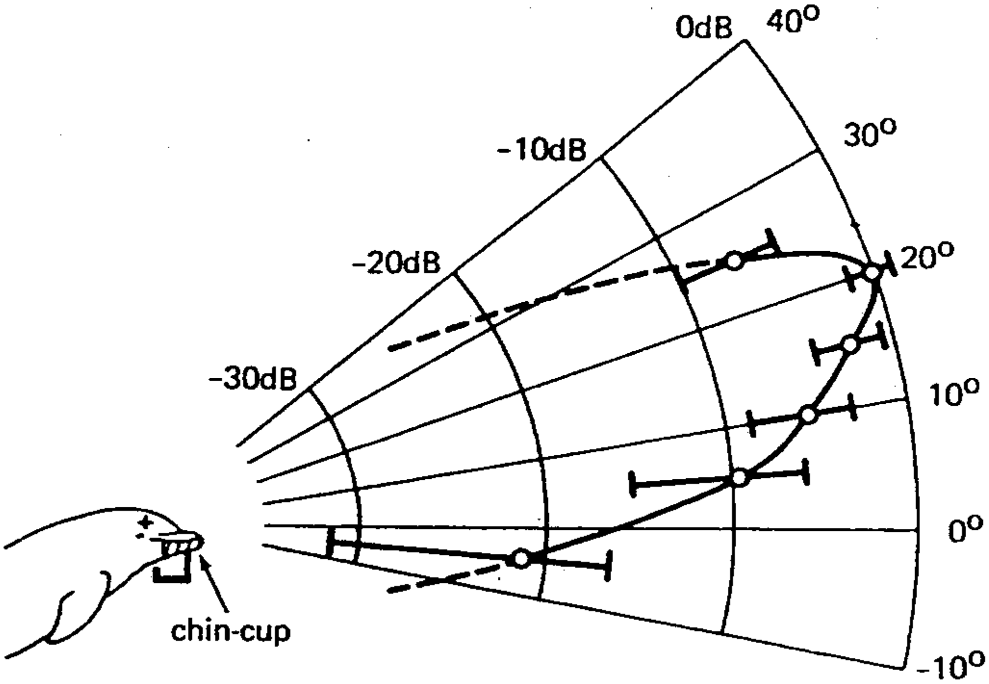

Fig. 7. Broadband beam patterns for the echolocation signals of bottlenose dolphins, *Tursiops truncatus*, in the vertical plane (Reprinted with permission from Au et al. 1978 ©Acoustical Society of America)

unidirectional. Sonar engineers call this the receiving directivity index (Urick 1983), and they define it as

$$DI = 10 \log \frac{SNR\ directional\ receiver}{SNR\ omnidirectional\ receiver} \tag{11}$$

Another way to put this is that the noise masking level for a directional receiver equals the NL (omnidirectional) - DI.

3.3.4

Using the Noise-Limited Active Sonar Equation to Estimate the Range of Dolphin Echolocation

A sonar with a sensitive receiver is typically limited by ambient noise rather than the inherent sensitivity of the receiver. A sonar that detects echoes from its own sounds is called an active sonar, and the performance of a sensitive active sonar is calculated from the noise limited *active sonar equation*. For simplicity, the following equation assumes that the signal is detected when the level of the echo equals or exceeds that of the noise:

$$\begin{aligned} &Echo\ level \geq noise\ masking\ level \\ &SL - 2TL + TS \geq NL - DI\ . \end{aligned} \tag{12}$$

The difference between the active and passive equations is that the active equation must account for the transmission loss from the sound to the target, the ratio of echo intensity to sound intensity incident on the target [*target strength* = TS = 10 log (intensity of reflected sound at 1 m)/(incident intensity)] and the transmission loss on the return of the echo to the receiver.

We now know enough to estimate the effective range of bottlenose dolphin sonar. For this example we will assume that a bottlenose dolphin in Kaneohe Bay, Hawaii emits a 220 dB echolocation click in order to detect a 2.54 cm diameter ball bearing 72 m away (remember that this is the demonstrated range at which this target could be detected). Let us start with the left half of Eq. (12). First we must estimate the transmission loss (Table 4). Au (1993) states that spherical spreading is a good approximation for transmission loss in this area. The equation for spherical spreading [Eq.(5)] is 20 log (range/reference range of 1 m). For a range of 72 m, this is 20 log (72) = 20 × 1.86 = 37 dB. Dolphins in Kaneohe Bay tend to use relatively high frequency clicks, so let us assume that this click had peak energy near 120 kHz. If the peak energy of the click was at 120 kHz, the absorption would be somewhere between 10^{-1} and 10^{-2} dB/m from Table 1. If we take an intermediate value of 3×10^{-2} dB/m, then the estimated loss for a 72 m path would be 2 dB.

We must be careful to ensure that the source level of the dolphin click is corrected to estimate the energy the dolphin actually hears from the echo. We will focus on the domain of time, and will need to take into account the physical processes of sound transmission and reflection from the target as well as the timing of the dolphin's auditory system. The most important of these factors is the short duration of the echoloca-

Table 4. Calculation of transmission loss (TL) using spherical spreading (20 log r) to 72 m

Δ Range	TL (dB)
20 log 72/1 m	37
Absorption	2
Total	39

tion clicks of dolphins compared with the integration time of dolphin hearing. For example, the peak to peak sound pressure level of 226 dB shown in Figure 6 occurred over just one wave of the click. At 120 kHz, this would correspond to a duration of 1/120 000 s = 8.3 µs. Au (1993) reviews evidence that dolphins integrate click energy over an interval of 265 µs. How does this compare with the changes in the click as it propagates and reflects off the target? As this click propagates, slight inhomogeneities in the water may create several ray paths between the dolphin and the target. As we saw for the finback pulse (Sect. 3.3.2), this may spread the energy of the pulse over a longer time period. As the click reflects from various parts of the target, this will also spread the energy of the pulse. The time it would take from when the pulse hits the front of the target to when it hits the rear of the target would be 0.0254 m / 1500 m/s = 16.9 µs. However, if dolphins integrate sound energy over an interval of 265 µs, then the timing of dolphin hearing will have the greatest impact on the perceived source level because the dolphin will integrate the click energy over a period more than an order of magnitude greater than the click duration. The ideal way to calculate this energy would be to integrate the energy of one click over 265 µs. We can approximate this by assuming that most of the click energy occurs over a duration of 8.3 µs and averaging this over 265 µs. By Eq.(10) this correction would be SL' = SL + 10 log (8.3/265) = SL - 15 dB. The target strength of the 2.54 cm diameter ball bearing used as the target has been measured at -42 dB (Au 1993; p 147).

The simplified form of the active sonar equation [Eq.(12)] that we are using assumes that the dolphin will detect the click when the energy from the echo equals the noise level. We will now use the right half of Eq.(12) to estimate whether the dolphin could detect the target at a range of 100 m (Table 6). The noise level present in Kaneohe Bay at 120 kHz is near 54 dB re 1 $\mu Pa^2/Hz$ (Au 1993). This level is given as a *spectrum* level which is the level for a 1 Hz band. This must be corrected for the actual band over which the dolphin receives the click. These clicks tend to have a bandwidth of about 40 kHz (e.g., Figure 6). This bandwidth is quite close to the bandwidth over which bottlenose dolphins integrate sound energy at this frequency (Au and Moore 1990). Thus, both the bandwidth of dolphin hearing and of the click would suggest that we estimate the noise

Table 5. Calculation in decibels of received level (RL) from the left-hand side of the active sonar equation [Eq.(12)]: RL = SL -2TL + TS

SL	220
Correction for integration time	-15
-2 TL	-78
+ TS	-42
= RL	85

Table 6. Calculation in decibels of noise level from the right-hand side of the active sonar equation [Eq. (12)]

Spectrum noise level at 120kHz	54
Correction for bandwith of click	+46
Correction for directivity of dolphin hearing	-20
Noise level	80

level for a band of about 40 kHz around 120 kHz. If we assume that the noise level at 120 kHz is representative, then we can use Eq. (9) to correct from the 1 Hz spectrum level to a 40-kHz band level as follows: Band level = spectrum level + 10 log (40 000/1) = 54+46 dB. The highly directional hearing of dolphins at 120 kHz gives a receiving directivity index of 20 dB at 120 kHz (Au 1993). This reduces the effective noise level by 20 dB.

These rough calculations would suggest that the dolphin would hear an 85 dB echo from a 2.54 cm ball at a range of 72 m, compared with a noise level of about 80 dB. This would indicate that the dolphin detects the echo at a signal to noise ratio of about 5 dB. This estimate is close to the theoretical detection threshold where the energy of the echo equals the ambient noise (0 dB SNR), and is closer than the comparison between the sonar equation and ray theory for the finback pulses. This may stem from the way the numbers in the dolphin active sonar equation were measured for a very specific application. However, Murchison (1980) points out that the dolphin click may reflect off the sea floor, sea surface, and any other inhomogeneities in its beam. Reverberation from these sources may raise the noise floor above the ambient sound from sources other than the dolphin, and this may mean that the dolphin's detection occurs at a lower signal to noise ratio than would be estimated ignoring reverberation.

Now it is the rare dolphin that spends its days echolocating on ball bearings. The kinds of targets of biological relevance for odontocetes include prey, predators, obstacles, and the seafloor and sea surface. Targets of biological importance may have echoes that differ from those of artificial targets. There has been considerable research by bioacousticians analyzing echo information from manmade sonars in order to classify biological targets (for a recent review see Stanton et al. 1995). Echolocating dolphins use subtle details of the returning echo to classify artificial targets (Helweg et al. 1996), and they may select or classify targets in their natural environment the same way. However, we know little about how dolphins use their sonar to detect or select prey or predators. Some animals have gas-filled cavities such as the lungs of mammals or the swim bladders of fish. The gas—water interface reflects sound energy and these gas-filled cavities provide good sonar targets. Swim bladders also have a resonance much lower in frequency than would be predicted by the $f = c/2\pi r$ calculation for rigid spheres. For example, a small anchovy at 1 atm of pressure had a resonant frequency of 1275 Hz (Batzler and Pickwell 1970). Little is currently known about whether odontocetes may modify their sonar signals in order to take advantage of these features of biologically important sonar targets.

Most animals have a density similar to water, and animals such as fish without swim bladders, squid, copepods, or krill will have lower target strengths than air-filled targets such as a swim bladder fish. In spite of the potentially low target strength of squid, many biologists have hypothesized that sperm whales may use their clicks, which are lower in frequency than those of dolphins, to echolocate on their prey, squid, in the deep ocean. Goold and Jones (1995) present a rough estimate based upon the sonar equation, suggesting that echoes from sperm whale clicks reflecting off of squid might be detectable to ranges of up to hundreds of meters. This estimate rests upon some untested assumptions and nothing is known about whether or how sperm whales echolocate, so confirmation of these results will have to rely upon direct empirical studies. It will be a significant challenge to attempt to study the sensory mechanisms sperm whales use to forage as they dive hundreds of meters deep for up to an hour or more.

4

Hearing Under the Sea: How Do Marine Animals Receive Acoustic Signals?

In order to detect sound, animals require a receptor that can transduce the forces of particle motion or pressure changes into neural signals. Most of these *mechanoreceptors* in species as diverse as invertebrates, fish, and mammals involve cells with hair-like *cilia* on their surfaces. Movement of these cilia modify the voltage between the inside and the outside of the receptor cells, and this voltage difference can modify the rate of action potentials that communicate the signal to other parts of the nervous system. If the cilia are on the surface of the body, they can detect the flow of water or hydrodynamic forces along the animal's body. Many invertebrate and vertebrate species also have internal sensory organs containing sensory cells with cilia. The stimulus that excites the sensory cells depends upon the structure of the sensory organ. For example, the semicircular canals detect fluid motion within the canal induced by rotation of the head. There are other sensory organs in which the cilia are coupled to a dense mass. When the body of an animal accelerates, this mass will tend to remain stationary. The inertial forces on this mass will bend the cilia, generating a sensory signal proportional to the acceleration of the animal. If this organ can detect the acceleration forces of gravity, it may function for maintenance of equilibrium. In invertebrates, the fluid-filled sensory organ which contains a dense mass is called the *statocyst*. The statocyst is known to be involved in orientation and equilibrium in some invertebrate species. While we know from behavioral conditioning experiments that marine invertebrates like the lobster *Homarus americanus* can hear, there have been few studies to demonstrate which organs are responsible.

The inner ear of fishes contains sensory organs in which heavy calcified masses called the *otoliths* are in close contact with the cilia of sensory cells. Hawkins and Myrberg (1983) reviewed experiments showing that these otolith organs are sensitive to sound. Most marine organisms are about the same density as seawater, which makes them acoustically transparent. This means that when a marine organism is exposed to sound, the particle displacement in the surrounding medium may cause the whole body of the animal to move slightly back and forth. The dense mass moves less, generating a force that stimulates the coupled sensory cells. This is a mechanism for detecting particle motion, which is a vector quantity with both a magnitude and an associated direction.

It has been suggested that directional hearing in fish may stem from orientation-specific sensory cells detecting particular directions of particle motion (Popper and Platt 1993). For a review of directional hearing in fish and other nonmammalian vertebrates, consult Fay and Feng (1987).

There is great variability in the hearing ranges of fish as is indicated in the middle section of Figure 5, which shows audiograms of a variety of fish species. This figure also includes an invertebrate and two cetaceans. Many fish appear to rely primarily on the detection of particle motion that was just described in the preceding paragraph. They have relatively low sensitivity which declines rapidly above 100-200 Hz. The toadfish indicated in Figure 5 by the line with the diamond symbols, is an example of this kind of audiogram. Some other species of fish have evolved specializations for hearing involving a coupling between a gas-filled cavity such as the swim bladder and the ear. Gas is highly compressible and is much less dense than water, so when a gas-filled space is ensonified, it will reverberate with the pressure fluctuations created by sound. The motion of the swim bladder may then be conducted to the ear, amplifying an acoustic signal for the ear to detect. This allows fishes with these specializations to detect the pressure fluctuations induced by sound. Fishes with these specializations have more sensitive hearing and better high frequency hearing. The importance of the coupling between the swim bladder and the inner ear can be seen by comparing the hearing of two genera of squirrelfish. The fish with the most sensitive hearing indicated in Figure 5 is a squirrelfish of the genus *Myripristis*, which is indicated by a line with small filled retangles. There is a good coupling between the anterior swim bladder and the inner ear in this genus. By comparison, even though the genus *Adioryx* is a member of the same family of fish, it has less sensitive hearing, particularly at higher frequencies, as is indicated by the line with circle symbols. The swim bladder in *Adioryx* is not as well coupled with the inner ear as in *Myripristis*, indicating how significant an effect this coupling can have on hearing. Other groups of fishes have independently evolved other forms of coupling between the swim bladder and the inner ear. For example, the goldfish has a series of bones coupling the swim bladder and the ear. Even though the mechanism for the coupling differs from *Myripristis*, the goldfish also has better hearing, particularly at high frequencies, than unspecialized fish such as the toadfish, *Opsanus*.

The terrestrial mammalian ear is typically divided into three sections. The *outer ear* is a canal which ends at the *eardrum* or *tympanic membrane*. The eardrum moves due to the pressure fluctuations of sound in air. The *middle ear* contains a series of bones which couples this movement of the eardrum to the inner ear. The *inner ear* of mammals contains the *cochlea*, which is the organ in which sound energy is converted into neural signals. Sound enters the cochlea via the *oval window* and causes a membrane, called the *basilar membrane*, to vibrate. This membrane is mechanically tuned to vibrate at different frequencies. Near the oval window, the basilar membrane is stiff and narrow, causing it to vibrate when excited with high frequencies. Farther into the cochlea, the basilar membrane becomes wider and floppier, making it more sensitive to lower frequencies. The mammalian ear thus appears to encode sound differently from the fish ear. Sound pressure is the primary stimulus and the basilar membrane acts as series of filters, each of which only respond to a small band of frequencies. Sensory cells at dif ferent positions along the basilar membrane are excited by different frequencies, and their rate of firing is proportional to the amount of sound energy in the frequency band to which they are sensitive.

Marine mammals share basic patterns of mammalian hearing, but cetacean ears have adaptations for marine life. The eardrum and middle ear in terrestrial mammals functions to efficiently transmit airborne sound to the inner ear where the sound is detected in a fluid. Such matching is not required for an animal living in the water, and cetaceans do not have an air-filled external ear canal. The problem for cetaceans is isolating the ears acoustically, and the inner ear is surrounded by an extremely dense bone which is isolated from the skull. Norris (1968) proposed that sound enters the dolphin head through a thin section of bone in the lower jaw and is conducted to the inner ear via fatty tissue which acts as a waveguide. This has recently been verified by Aroyan (1996) who developed a technique to map acoustic parameters using data from a computerized tomography (CT) scan of a dolphin's head provided by Cranford (1992).

It is obvious that most of the energy of an acoustic signal must occur within the hearing range of an animal to be an effective stimulus, and there is a correlation between the frequencies at which most fish species can hear best and the frequencies typical of their vocalizations (e.g., Stabentheimer 1988). Given the small sizes of fish, it is striking how low in frequency most of their calls are, with most energy typically below 1 kHz. This clearly matches the auditory sensitivities illustrated in Figure 5. As Figures 5 and 6 show, there is also a close correspondence between the frequencies of best hearing for bottlenose dolphins and harbor porpoises and the dominant frequencies of their echolocation clicks. The frequency range of hearing has never been tested in baleen whales. Hearing is usually tested by training an animal, and baleen whales are so big that only a few have been kept for short periods in captivity. However, both their low frequency vocalizations and the frequency tuning of their cochlea suggests they are specialized for low frequency hearing (Ketten 1994).

The hearing abilities of animals have not evolved exclusively for detecting sounds of conspecifics. For example, the goldfish, *Carassius auratus*, has good hearing for a fish (Figure 5), but has never been heard to produce a sound (Popper and Platt 1993). Fish must also use passive listening to learn about their biological and physical environment. For example, it has been suggested that the ability to detect high frequencies may have evolved in fish to allow them to detect the loud echolocation clicks of their odontocete predators (Offut 1968). Some recent research suggests that fish such as alewives, herring, and cod are able to detect intense sounds of frequencies much higher than is typical of their vocalizations. For example, Astrup and Møhl (1993) provide evidence that cod, *Gadus morhua*, detect short 38 kHz pulses at 194 dB re 1 µPa. This is a very high frequency for fish to detect, and the only known natural sources of this intensity and frequency are the clicks of echolocating toothed whales. Cod may be able to detect the loudest clicks of echolocating toothed whales at ranges of 10–30 m. Both alewives, *Alosa pseudoharengus*, and blueback herring, *Alosa aestivalis*, formed tighter schools and moved away from playback of sounds from 110 to 140 kHz at levels above 160 dB re 1 µPa (alewives; Dunning et al. 1992) to 180 dB re 1 µPa (herring; Nestler et al. 1992). While these results are suggestive, it remains to be seen how fish respond to the echolocation sounds of their actual predators. Given the extensive evidence of elaborate strategies and countermeasures between echolocating bats and their insect prey (e.g., Surlykke 1988), it is amazing how little comparable evidence is available for marine echolocators.

Perhaps more interesting than the obvious frequency match between signal and receptor is the comparison of time vs. frequency cues in fish vs. mammals. Many fish calls are either amplitude modulated or are composed of pulses. Hawkins and Myrberg (1983) review studies suggesting that fish are remarkably sensitive to slight variation in the timing and duration of their calls, while frequencies can be changed considerably with little change in response. Fish do not appear to be very sensitive to changes in frequency, and they do not have a peripheral frequency analyzer as highly developed as the mammalian cochlea. Most species of fish whose auditory frequency discrimination has been tested are capable of discriminating tones that differ by 5–10 % (Hawkins 1981). Instead of relying so heavily on a spatially organized array of frequency tuned sensory cells as in mammals, fish apparently rely more upon synchronizing neural responses with the temporal characteristics of the acoustic signal. By contrast, mammalian hearing is highly sensitive to frequency. Among mammals, dolphins have extraordinarily good abilities of discriminating different frequencies, and can detect a change of as little as 0.2 % in frequency (Thompson and Herman 1975). The number of sensory cells in their inner ear is higher than that for the human ear (Ketten 1994). The frequency range in which dolphins can discriminate frequencies the best is near 10 kHz. This matches the frequency range of dolphin whistles, which are frequency modulated tonal sounds. Most researchers who have studied whistles have concluded that frequency cues are critical elements of these communication signals.

5

Communicative Significance of Marine Animal Sounds

Most of the research in the previous section stems from studies in which captive animals are trained to respond to artificial stimuli, such as the pure tones used to measure hearing sensitivity. Marine mammals are well known for being easily trainable, but both invertebrates (Offut 1970) and fish (e.g., Tavolga et al. 1981) can also be trained to respond to sound for studies of hearing. Experimental studies of captive animals working on artificial problems have also been crucial for demonstrating the echolocation abilities of toothed whales. Schusterman (1980) reviews many of the conditioning techniques used to study echolocation in marine mammals. A very different research method has been used for most studies of animal communication. The ethological tradition of studying animal communication emphasizes studying animals in naturalistic settings. Ethologists start with a catalog of behaviors or vocalizations typical of their study species. As mentioned earlier (Sect. 1.3), the early phase of marine bioacoustics consisted primarily of cataloging the vocalizations of different marine species. Ethologists use this kind of catalog of species-specific displays as a starting point. Once the displays are well defined, ethologists observe animals to define the contexts in which an animal makes a particular display, and to define the responses of animals that receive the signal. Descriptive studies often find that a response may frequently follow a particular signal, but these studies cannot test whether a signal actually causes the response. These associations are tested in experiments in which the investigator presents a replicate of a signal and observes how an animal responds. There is a long tradition of testing responses of fish to artificial visual (Tinbergen 1951) or acoustic (Moulton 1956) stimuli in order to tease apart the pattern of signal and response that make up a communication system. The acoustic version of these experiments involves playbacks of recorded sound to animals in the environment in which the communication system usually functions (Nelson and Marler 1990). Sound playback experiments of this sort are critical for identifying which features elicit which response, and for defining sound categories in terms of their function in natural settings.

The logic of underwater playback experiments is the same as the airborne version (see Hopp and Morton, this Volume). Since vision is so limited underwater, it is often easier to set up realistic experiments underwater where the subject cannot see as far as the range of the speaker and has no reason not to expect the likely presence of the animal whose sounds are being played. Playback of natural vocalizations allows one to study the function of animal vocalizations. Synthetic stimuli are also often very useful for sound playbacks. This requires the ability to extract the acoustic features one thinks are relevant, modify one or more features, and resynthesize the modified sound (see discussion by Beeman, this Volume). The technical problems of accurate reproduction of playback stimuli are alleviated by a service of the US Navy. The Navy runs an Underwater Sound Reference Detachment (USRD, Orlando Florida) which maintains a stock of calibrated underwater sound projectors and reference hydrophones (USRD 1982). With careful selection of recorder and power amplifier, these projectors allow highly accurate reproduction of most marine biological acoustic signals. However, one must always monitor the playback stimuli even more carefully than in airborne applications, because underwater sounds cannot be heard very well without electronic monitoring. Researchers playing back sounds in air are more likely to detect technical problems with the unaided ear.

Several examples of communication in marine invertebrates, fish, and marine mammals will now be discussed.

5.1
Invertebrates

Little is known about the communicative significance of acoustic displays in marine invertebrates. Interesting work has been conducted with snapping shrimp of the genera *Crangon* and *Synalpheus*. These shrimp produce loud snapping sounds which are reported to have primary energy between 2 and 15 kHz (Everest et al. 1948). MacGinitie and MacGinitie (1949) suggested that snapping shrimp of the genus *Crangon* produce a sound intense enough to stun their prey, and that these snaps function in feeding. Later work emphasizes the role of snapping as an aggressive display, particularly in defense of a shelter, and suggests that the water jet may be as important a stimulus as the acoustic attributes of the display (Hazlett and Winn 1962; Nolan and Salmon 1970; Schein 1977). In the laboratory, when two snapping shrimp of the genus *Alpheus* are put in a jar with one shelter, they will usually go through a series of threats, including cocking the claw and snapping. A shrimp may damage the leg or antenna of an adversary if it makes contact as it snaps its claw. Most fights appear to be resolved by an exchange of ritualized threats without injury, however. Larger animals usually win over smaller ones. In contests between individuals belonging to different species but having the same body size, the species with the larger claw tends to win. This suggests that shrimp pay particular attention to the claw when assessing the fighting ability of an adversary. It appears that the visual appearance, acoustic properties of the snap, and tactile properties of the water jet are used for this fighting assessment. Less is known about perception of underwater sound in marine invertebrates than about production, and use of this sensory channel for communication remains underexplored in marine invertebrates compared with vision and the chemical sense.

5.2
Fish

Fish were early subjects of ethological research. Even after von Frisch (1938) demonstrated hearing in fish, most early ethological study of communication in fish emphasized visual stimuli such as coloration and markings on the body (e.g., Baerends and Baerends-van Roon 1950). However, acoustic signals may play an important communicative role even in fish with pronounced coloration displays. For example, Myrberg (1972) showed that bicolor damselfish (*Pomacentrus partitus*) produce different sounds and coloration patterns when they are courting, fighting, or feeding. These fish were studied both in a large aquarium in the laboratory, where every detail of behavior could be observed, and on a coral reef in the sea, using an underwater video system. Adult males of this species are very territorial, and their stable residence allowed them to be identified in the wild over many months. Males compete to attract females that are ready to spawn, and they have specific coloration, motion patterns, and chirp or grunt sounds associated with different phases of their courtship displays. When bicolor damselfish are engaged in a hostile or agonistic interaction, they have a very different coloration pattern, produce a *pop* sound, and engage in a different set of behaviors. When feeding, these fish have yet another coloration pattern and produce a faint stridulation sound different from either the courtship or agonistic sounds. Males will often attack a fish approaching their territory, and presumably a male produces courtship displays to a female to signal that he will not attack her, to signal that he is ready to mate, and to influence the female's choice of a mate. If a male detects that courtship is going on nearby, he may start producing competitive courtship displays as well (Kenyon 1994).

In order to test whether these damselfish sounds had a signal function, Myrberg (1972) played recordings back to males both in the field and in the laboratory. Playback of the courtship sounds had a pronounced effect on these males. Within 30–60 s of the onset of courtship sounds, males tended to switch from the normal coloration pattern to one of the two courtship patterns (Myrberg 1972). These playbacks of courtship sounds also elicited high rates of courtship behaviors and sounds from these males. Playback of the agonistic pops to males which were engaged in some courtship behavior, by contrast, inhibited both courtship acts and sounds. Spanier (1979) played back sounds of four different species of damselfishes, and found that each species responded more strongly to sounds of conspecifics. In keeping with the proposed importance of temporal cues for acoustic communication in fish, Spanier (1979) found that the most important acoustic features for this discrimination were the pulse interval and number of pulses in the call.

Myrberg's (1972) study of bicolor damselfish concentrated on the behavior and responses of males. Myrberg et al. (1986) focused on responses of females to playback of courtship chirps. This kind of field experiment relies heavily upon detailed observational data in order to optimize experimental design. For example, earlier work had shown that females tend to spawn at sunrise in the third quarter of the lunar cycle (Schmale 1981). In order to guarantee a reasonable number of ovulating females, the playbacks were limited to sunrise during the three peak days of spawning. The first playback experiment contrasted chirps of two males, one of which was 4 mm larger than the other. This larger male appeared to be more attractive to females, as he had more egg batches in his nest. The peak frequency of chirps from the larger male was 710 Hz, that from the smaller male 780 Hz, a frequency difference likely to be discriminable by fish. Of 21 females tested, 15 swam to the playback of the larger male and only two females swam towards the smaller male. A second playback series compared responses of females to chirps of conspecifics with either congeneric chirps or synthetic chirp-like sounds. All 14 of the females in this second playback series chose the chirps of conspecifics. These results show that females not only can use chirps to find a mating partner of the appropriate species, but also to select a mate from among several conspecifics.

Charles Darwin (1871) coined the term "sexual selection" to describe the evolutionary selection pressures for traits that are concerned with increasing mating success. There are two ways sexual selection can work. It can increase the ability of an animal to compete with a conspecific of the same sex for fertilization of a member of the opposite sex (intrasexual selection) or it can increase the likelihood that an animal will be chosen by a potential mate (intersexual selection). The evidence just discussed for bicolor damselfish would emphasize intersexual selection for the evolution of courtship chirps. In the bicolor damselfish, as in most animal species, it is the male sex that produces courtship displays and the female sex that selects a male for mating. The basic question for the evolution of displays by intersexual selection is why are females choosing particular features of the male display? Three factors that may influence female choice are: (1) correlations between a feature of the display and the quality of the male; (2) sensory bias of the female; and (3) positive feedback between a female preference and features of a male display. The first factor appears to be most important for the evolution of the chirps of bicolor damselfish, and discussion of the other two factors will be postponed for more appropriate species.

One important feature of quality in male fish appears to be body size, as females of many species tend to select larger males as mates (e.g., Schmale 1981, for bicolor damselfish). Myrberg et al. (1993) demonstrated a strong correlation between the body size of bicolor damselfish and the fundamental frequency of the chirp sound. Myrberg et al. (1993) suggested that differences in the peak frequency of chirps result from differences in the volume of the swim bladder. If females are selecting larger males that have chirps with the lowest peak frequency, then this will create a selection pressure for males to make the lowest chirps they can. However, if the minimum peak frequency a male can produce is constrained by the volume of his swim bladder and if the swim bladder volume correlates with body size, then males may be constrained to produce an honest advertisement of their body size. Similar cases of selection for low frequency indicators of body size are also known for a diverse array of vertebrates, and may involve fighting assessment between males as well as mate choice (e.g., Davies and Halliday 1978, for anurans; Clutton-Brock and Albon 1979, for a mammal). The reliability of the association between peak frequency and body size may have selected for females to attend to this frequency cue, even though fish are thought in general to be more sensitive to temporal features of their sounds.

Studies of communication in the oyster toadfish:, *Opsanus tau*, also include responses of females to the courtship sounds of males. Winn (1972) describes two primary acoustic signals from the oyster toadfish: the grunt and the boatwhistle. The grunt is produced during aggressive interactions, with more grunts produced in more intense interactions. Male toadfish produce the boatwhistle sound when they establish nests at the beginning of the breeding season. While grunts are usually produced in the context of aggressive interactions, boatwhistle sounds are produced at regular intervals by a male even when he is alone. Winn conducted a series of playback experiments in order to test whether males produce this call to attract females to lay eggs in their nests. Initial tests showed that toadfish seldom respond before evening, so Winn restricted the playbacks to this evening response time. He made pens and put an open can similar to a toadfish nest in each of the four corners of the pen. Speakers were attached to each of these cans. He then introduced a spawning male and female into the center of the pen and played boatwhistle sounds from the two of the four speakers. The other two silent cans were considered control cans. None of the females that had no eggs because they had already spawned entered any of the cans. Of the 66 males tested, none entered a control can and only four entered a can with boatwhistle sounds. However, of the 44 females with eggs, 15 entered boatwhistle cans, one entered a control can, and 28 did not enter a can. This suggests that females that are ready to spawn are attracted to the boatwhistle sound.

Features associated with effort or cost appear to be important in the evolution of the boatwhistle display. Boatwhistles are very loud and prolonged compared with most fish vocalizations. Fine (1978) suggests that the fundamental frequency of the harmonic part of the boatwhistle call is affected more by the rate of contraction of sound-producing muscles rather than by the volume of the swim bladder. If so, then the frequency of boatwhistles may not be a reliable indicator of the size of the displaying fish, as was suggested for the bicolor damselfish. If the fundamental frequency of the boatwhistle is driven by the rate of muscle contraction, then the rate of contraction may correlate with effort of the displaying fish. The fundamental frequency of boatwhistles varies from < 150 Hz early in the breeding season to > 250 Hz nearer the peak of the season, and duration shows a similar increase (Fine 1978). When a male toadfish sees a female or hears an indication that a female may be nearby, he increases his own display effort in order to attract the female. While most males produced boatwhistles at rates of about 7/min, they increase their calling rate when they hear playbacks of boatwhistles at rates greater than 12 boatwhistles/min (Winn 1972). Males also increase their rate of boatwhistle calls when a female comes within a meter or so (Gray and Winn 1961; Fish 1972). All of these responses of males indicate that females may select a mate based upon his display effort.

Ryan et al. (1990) argue that preexisting biases in the sensory systems of females may be an important factor in the evolution of displays by sexual selection. Most communication systems show a match between the frequency range of the signals and the receptors, but there appears to be a mismatch for boatwhistles which may have influenced some of the boatwhistles, acoustic characteristics. While male toadfish respond to playbacks of tone bursts in the range 180–400 Hz as if they were boatwhistles, they do not respond to sounds that contain the lower frequencies of 90–100 Hz (Winn 1972). This suggests that there is a lower limit in frequency below which boatwhistles become less stimulatory to males. This is particularly interesting because Fish and Offut (1972) and Fine (1981) present evidence that toadfish are most sensitive to sounds in the frequency range from 40 to 90 Hz, with sensitivity decreasing rapidly at higher frequencies (see Figure 5). If females have the same kind of bias for preferring boatwhistle sounds in a frequency range to which they are less sensitive, as was demonstrated by Winn (1972) for males, then this may force males to put more effort into the display, influencing some features of the boatwhistle, such as its extraordinary loudness.

Communication is often analyzed as an exchange of one signal and an immediate response. For example, Myrberg (1972) analyzed the functions of a damselfish display by comparing which displays immediately preceded or followed a particular display. This may be appropriate for many signals, but it does not seem appropriate for analyzing the boatwhistle which is produced spontaneously at regular intervals by males during the breeding season whether another animal is present or not. The boatwhistle of a toadfish is more likely to be followed by another boatwhistle from the same fish than by a response from a different fish. These kinds of signals have been called advertisement displays, and Winn (1972) suggests that the boatwhistle display is analogous to the songs of birds which are a well known reproductive advertisement display. The structure of advertisement displays cannot be understood simply in terms of an immediate response to one signal. One must consider more broadly how the signal is designed to manipulate choices of animals that hear the display (Krebs and Dawkins 1984). Advertisements are often produced in great quantity in order to modify the outcome of a choice that an animal may make over a long period of time. Advertisements are in general designed to be attention getting. For example, the boatwhistles of toadfish are loud, sustained, and repeated.

Two kinds of features that females might use in choosing a male have just been discussed. One is a direct correlation between the display and some physical attribute of male quality that will be important to the female. Female bicolor damselfish may choose a lower frequency as an indicator of large size of a male. Another kind of feature is related to the cost of the display. If producing the display is taxing or dangerous enough, the male who achieves the most intense display may be in the best condition. Female toadfish may use a variety of features to assess the level of effort a male is putting into his display.

5.3
Marine Mammals

5.3.1
Reproductive Advertisement Displays

Marine mammals also produce reproductive advertisement displays. The best known acoustic advertisement displays are called songs, which are usually defined as a sequence of notes that are repeated in a predictable pattern. Male seals of some species repeat acoustically complex songs during the breeding season. Songs are particularly common among seals that inhabit polar waters and that haul out on ice. The vocalizations of ringed seals, *Phoca hispida*, become more common along with agonistic behavior as the breeding season gets underway (Stirling 1973). The songs of bearded seals, *Erignathus barbatus*, are produced by sexually mature adult males (Ray et al. 1969). Bearded seal songs are heard frequently during the peak of the breeding season in May; but by July song is seldom heard. Male walruses, *Odobenus rosmarus*, also perform ritualized visual and acoustic displays near herds of females during their breeding season (Fay et al. 1981; Sjare and Stirling 1993). Males can inflate internal pouches that can produce a metallic bell-like sound (Schevill et al. 1966). Walruses make loud knock, whistle, and breathing sounds in air when they surface during these displays. When they dive, these males produce distinctive sounds underwater, usually a series of pulses followed by the gong- or bell-like sounds. Usually several males attend each female herd, so the relative roles of this display in intersexual vs. intrasexual behavior are not known (Sjare and Stirling 1993). Antarctic Weddell *(Leptonychotes wedelli)*, seals also have extensive vocal repertoires and males repeat underwater trills (rapid alternations of notes) during the breeding season. Males defend territories on traditional breeding colonies. These trills have been interpreted as territorial advertisement and defense calls (Thomas et al. 1983). Whether females may also use them in selecting a mate is unknown.

The songs of humpback whales are the best understood advertisement display in the cetaceans. These songs sound so beautifully musical to our human ears that they have been commercial bestsellers. Figure 8 shows a spectrogram of a humpback song made in Hawaiian waters during a period when songs contained up to nine themes. The third theme was not included in this song, but was in the next song of this whale, as is indicated by the star in the spectrogram. Each theme is made up of repeated phrases or series of sounds lasting on the order of 15 s. Phrases of one theme repeat a variable number of times before a new theme is heard. In Figure 8, the phrase boundaries are marked by vertical lines. Humpbacks tend to sing themes in a particular order, and it often takes about 10 min before a singer comes back to the initial theme.

The observational key to our understanding of humpback song lies in the ability of biologists to find and follow a singing humpback whale. The first step is to use a small boat to monitor underwater sound in different areas within a breeding ground until the song of one whale is much louder than any other. Singers often surface to breathe once per song during a particular theme, and they *blow* or breathe during the silent intervals between notes (Tyack 1981). When the singer reaches this part of the song, it can be

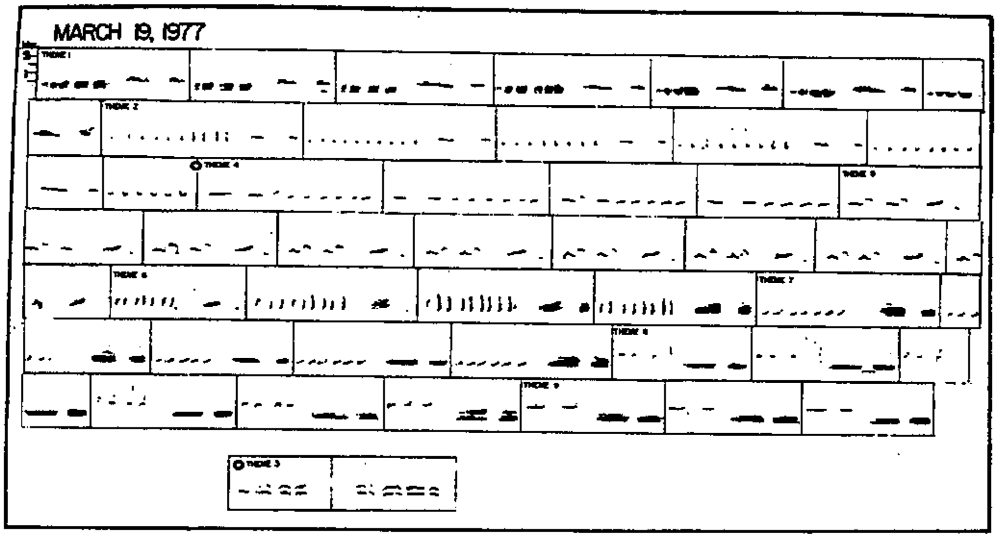

Fig. 8. Spectrogram of the song of a humpback whale, *Megaptera novaeangliae*. This song was recorded from a lone humpback on 19 March 1977 in the Hawaiian Islands. Each *line* represents 120 s, and this song took seven lines or 14 minutes before repeating the initial theme. The song at this time had up to nine themes in it. The start of each theme is marked on the spectrogram. Each theme is made up of repeated phrases, and the boundary between phrases is marked by vertical lines. This particular song did not include theme 3, but the next song in this sequence did, and is indicated at the bottom of the spectrogram. (reprinted from Payne et al. 1983, with permission)

located by careful visual scanning from the boat that is monitoring the song. The song gets fainter seconds before the singer breaks the surface to breathe, and this often allows one to identify one surfacing whale as the singer. When one approaches the singer, the sound of the song is often loud enough to be heard through the hull of the boat. Once a singer has been identified in this way, its sex can be determined by underwater photography of the genital slit (Glockner 1983) or by taking a small tissue sample for genetic determination of sex (Baker et al. 1991; Palsbøll et al. 1992). The continuous vocalizations and predictable surfacing behavior of singers allows them to be followed for periods of hours. These observations have shown that almost all singing humpbacks are lone adult males, and they repeat songs in bouts that can last for hours.

Interactions between whales can take so long and can occur over such great distances that special techniques are required to document them. Observation from elevated sites on land has been important for studying species, such as humpbacks, that concentrate near coastal waters. Observers on land can use a surveyor's theodolite to pinpoint the location of each whale surfacing and can communicate by radio with vessels that can obtain more detailed behavioral and acoustic data while they follow whale groups (Tyack 1981). These visual locations can also be linked to acoustic locations from arrays of hydrophones (Frankel et al. 1989). These techniques have documented responses of singing whales with groups nearly 10 km away and are well suited to observing whales for periods up to 10 h. The interactions of whales are so much slower than our own pace, that it is often necessary to make a plot of movement patterns and behavioral displays in order to make sense out of an interaction that took many hours to unfold.

These kinds of behavioral observations have shown that singing humpback whales appear motivated to join with nearby whales, and singers often swim towards other whales while still singing (Tyack 1981). Singing humpbacks usually stop singing when they join with other whales. Females have occasionally been observed to approach and join with a singing humpback; behavior associated with sexual activity has been observed after the female joins the singer (Tyack 1981). Aggressive behavior has often been seen after a singer joins with another male. Males may approach and join with a singer to initiate these competitive interactions. After a male has joined with a singer, the singer may then stop singing and leave, while the whale that joined may start singing himself. However, most groups of whales seem to avoid the potentially aggressive singers. While breeding males are not territorial on the breeding ground, song mediates both competitive interactions between males and some associations between males and females. Humpback song appears to play a role both in male—male competition for mates (intrasexual selection) and perhaps in female choice of a mate (intersexual selection).

There appears to be a strong force for vocal convergence in the songs of humpback whales on a breeding area at any one time, coupled with progressive change in all aspects of the song over time (Payne et al. 1983; Payne and Payne 1985). Recordings of humpback song made from different whales in the same breeding area at the same time are quite similar. At any one time, all of the singers within a breeding area sing the same themes in the same order, and the individual sounds that make up the song are quite similar. However, the song changes dramatically from month to month and from year to year. For example, in hundreds of recordings made later in the spring of 1977 and for years afterwards, theme three from Figure 8 was never heard after the end of March 1977. There is no indication that these changes in the song reflect changes in the message; the whales appear to be engaged in similar interactions even as the song changes.

The combination of complexity and progressive changes in humpback song suggest that sexual selection may select for complexity of the acoustic display per se. As Darwin (1871) pointed out for other species, we clearly may have to thank the aesthetic sensibilities of generations of female humpbacks for the complexity and musical features of the males' songs. Fisher (1958) explained the evolution of this kind of extraordinarily complex and beautiful secondary sexual character in terms of a *runaway process* of sexual selection. The runaway process emphasizes positive feedback between the female preference and the elaboration of a male display. Let us start by assuming that females have developed a preference for an acoustic display with a particular feature. This preference could arise because the display was correlated with some valuable male trait, the display could make the male more easy to find, or females could simply have some bias to respond preferentially to a particular stimulus. Whatever the origin of the preference, the tendency for females with stronger preferences to mate with males with the feature means that genes for the preference will covary with genes for the feature. If females on average select males with extreme development of the feature, then the next generation will have more sons with the exaggerated feature and more females with the preference. This creates a positive feedback loop, potentially producing a runaway process leading to extreme and exaggerated development of secondary sexual characters in males and preferences in females.

Male humpback whales appear to have two alternate strategies for gaining access to a female. They may sing in order to attract a female or they may join a group in which a female is already with one or more males. Males in these larger groups may fight for the position closest to the female in the group. During these fights, a set of sounds is heard that differ from song. These sounds are called social sounds. As with the grunts of toadfish, the more intense the aggressive interaction, the greater the number of social sounds heard (Silber 1986). Singing humpbacks may stop singing and make a beeline to join these groups from distances as far as 10 km (Tyack and Whitehead 1983). Groups of one to two adults without calves (and presumed to be males) also have been observed to join these competitive groups. It is unlikely that any cues other than acoustic ones such as the social sounds are detectable from such ranges.

Tyack (1983) conducted playback experiments to test whether the differential responses of different kinds of humpback social group to song or social sound were in fact mediated by these sounds. Techniques had already been established to follow each group and to monitor approach and avoidance as described above. The underwater sound projector and amplifier selected for this experiment were powerful enough to approach the source level of singing humpbacks, yet were portable enough to be deployed from 4–5 m boats. The two stimuli used were song and social sounds, and these were played back to lone singers, groups of one to two adults without a calf, groups of one to two adults with a calf, and competitive groups of three or more adults. While it was difficult to build large sample sizes for these playbacks, the results were consistent. During 9 out of the 16 social sound playbacks, singing whales or groups of one to two adults moved rapidly and directly to the playback boat, passing within meters of the underwater sound source. No whales rapidly approached the boat during the playbacks of song; in most of these, the target whale groups moved away. The results thus mirrored the responses observed when these sounds were produced by whales. Since two natural stimuli were used with no other control stimulus, one can only argue for differential response, not a highly specific response to each stimulus. Some of the critical features of this experiment were: (1) previous observation allowed prediction of responses; (2) predicted responses were strong and easy to score; and (3) limiting to two playback stimuli was crucial, given the difficulty of boosting sample size.

Other baleen whales also have been reported to produce reproductive advertisement displays. Bowhead whales, *Balaena mysticetus*, have been recorded producing songs as they migrate from their breeding grounds (Ljungblad et al. 1982). These whales spend their winter breeding season in Arctic waters such as the Bering Sea, where it is difficult to observe them, so we know little about behavior during the peak of the breeding season. While the individual sounds that make up bowhead songs are somewhat similar to those of humpbacks, the songs are simpler, lasting a minute or so. Like the songs of humpback whales, bowhead songs also change from year to year.

The long series of loud 20 Hz calls of finback whales also may be a reproductive advertisement display. They have a seasonal occurrence that closely matches the winter breeding season of these whales (Watkins et al. 1987). These 20 Hz series of finback whales are much simpler than the songs of bowheads and humpbacks. As has already been described, this appears to be a design feature for long-distance communication.

This matches what we know of the breeding pattern of finback whales. Humpback whales are thought to congregate in protected waters in the lee of tropical islands or banks for calving and breeding. A female in a breeding area can often hear many singers within a range of 10 km or so, in which most of the detail of humpback song is audible. Finback whales, on the other hand, are thought to disperse into tropical and temperate waters during their winter breeding season. While we actually know little of the spacing of finback whales during the breeding season, it appears likely that a female might have to listen for males over much longer ranges. This need for communication over long ranges may have created selection pressures for a simpler, more repetitive, loud and low frequency signal. If female finback whales had reasons for selecting large males and if low frequency vocalizations were a reliable indicator of size in finback males, then the low frequencies of these calls might also result from the kind of sexual selection described for bicolor damselfish and many other vertebrates. On the other hand, finback males are smaller on average than females, so selection for large size appears to be greater for females than males (Ralls 1976). In order to clarify these issues, we need better observations of vocalizing finbacks, responses of females to these 20 Hz series, and playback experiments varying frequency, source level, interval between pulses, etc.

Better evidence is needed on the role of reproductive advertisement vocalizations in mediating male—male competition and in mediating female choice for marine mammals. Real-time computerized acoustic source location allows direct measurement of the spacing of vocalizing males (Frankel et al. 1991). For species where females can also be tracked from their own vocalizations, this same technique could be used to follow females as they move through the field of advertising males. Data of this sort may help clarify the process of female choice and the acoustic and behavioral features which females may use to choose a mate. It will also be necessary to develop methods to identify which females are receptive. Female humpbacks may only be receptive for a short period of time around ovulation. Whaling data from the southern hemisphere indicates that nearly 50 % of adult females may be ovulating during one 10-day interval, with much lower rates of ovulation during most other parts of the breeding season (Chittleborough 1954). As with the toadfish, nonreceptive females are unlikely to approach a singing male. Playbacks to females should focus on receptive females, either during periods of peak ovulation or using a technique, such as a biopsy, to determine each subject's reproductive status.

While it is often difficult to apply sampling methods developed for visual observation of terrestrial animals (e.g. Altmann 1994) to marine bioacoustics, new instrumentation may also resolve some of these problems. Reliable and systematic sampling of vocal behavior will be improved by passive acoustic tracking of vocalizing animals, and sophisticated tags for animals that can sense vocalizations, the sound field of the animal, and other response measures. Animals that do not vocalize frequently and distinctively enough to allow acoustic tracking from their own vocalizations may be followed visually, or tracked after attachment of a tag. These techniques become much more powerful when used together to address specific scientific issues. For example, imagine tagging a female humpback as she swims into an area where all singers can be located acoustically. Suppose the tag attachment allows one to recover a biopsy that can later assess whether the female is receptive. Even a simple tag would allow one to track the female's movements through the field of singers, and more sophisticated tags might be able to record what she heard and her responses to different males.

5.3.2
Individual and Group Recognition with Special Emphasis on Sounds of Toothed Whales

Myrberg (1981) developed a general framework for analyzing communication in fish. He emphasized two kinds of intraspecific social interactions: finding and selecting mates and competition for mates or other resources. These are the kinds of interactions that have dominated the preceding section (Sect. 5.3.1). However, Myrberg also mentioned that a general framework must include the potential importance of social interactions directed toward the survival and reproduction of one's own offspring or more distantly related kin. If interactions with kin were important, they would create a selection pressure for some system for kin recognition. Blaustein and Waldman (1992) discuss evidence for kin recognition using chemical cues among amphibians, and similar chemical recognition of kin also occurs in some fish (Winberg and Olsén 1992). However, there is much less evidence for use of acoustic cues in kin recognition among fish, and Myrberg (1981) suggested that kin relationships among adults may be less important for fish than for some other animal groups, such as social insects, and some birds and mammals, including marine mammals. Many species with extensive parental care have a system for parent—offspring recognition. Parental care is limited in fish and rarely lasts for more than several weeks. Most models of the behavior of animals that aid one another through reciprocation also require some form of individual recognition. While the remarkable coordination of fish in a school clearly demonstrates impressive communicative mechanisms, there is little evidence of individual-specific relationships within such a school.

Myrberg and Riggio (1985) do provide evidence of individual recognition of chirp sounds in competitive interactions between male bicolored damselfish. As mentioned in Section 5.2, adult males in this species hold territories that are stable for months or years. This means that each territorial male will persistently be exposed to the displays of his neighbors. Myrberg and Riggio (1985) conducted playback experiments with a colony of bicolor damselfish on a small reef that contained five adult males. Chirp sounds were recorded from each of the males, and all five sets of chirps were played back to all five males. Each male showed a greatly reduced rate of competitive courtship displays to chirps from the nearest neighbor compared with all of the other males. However, this result might simply stem from increased habituation to the most familiar sound. In order to control for this, the sounds of the two nearest neighbors were played back, once from the neighbor's own territory and once from the territory of the other neighbor. Males responded much more strongly when the sound of a neighbor was played back from the wrong territory. This kind of playback design has yielded similar results in many other vertebrates, an effect known as the "dear enemy" phenomenon.

Many marine mammals do live in kin groups, and social interactions within these groups may have a powerful effect on fitness. The different structures of these cetacean societies create different kinds of problems of social living, and there appears to be a close connection between the structure of a cetacean society and the kinds of social communication that predominate in it. For example, stable groups are found in fish-eating killer whales, *Orcinus orca*, in the coastal waters of the Pacific Northwest, and these whales also have stable group-specific vocal repertoires. The only way a killer whale group, called a pod, changes composition is by birth, death, or rare fissions of very large groups (Bigg et al. 1987). Many of the calls of killer whales are stereotyped and stable over decades. These are called discrete calls. Each pod of killer whales has a group-specific repertoire of discrete calls that is stable for many years (Ford 1991). Each individual whale within a pod is thought to produce the entire call repertoire typical of that pod. Analysis of variation in call use within a pod suggests that some calls may be more common in resting groups, others more common in more active groups (Ford 1989). However, each discrete call in the pod's repertoire can be heard regardless of what the pod is doing. Different pods may share some discrete calls, but none share the entire call repertoire. The entire repertoire of a pod's discrete calls can thus be thought of as a group-specific vocal repertoire. Different pods may have ranges that overlap and may even associate together for hours or days before diverging. These group-specific call repertoires in killer whales are thought to indicate pod affiliation, maintain pod cohesion, and to coordinate activities of pod members.

Bottlenose dolphins (*Tursiops truncatus*) do not have stable groups as in resident killer whales, but rather live in a fission – fusion society in which group composition changes from hour to hour or even minute by minute. While dolphin groups are remarkably fluid, there may be strong and stable bonds between particular individuals. Some wild individual bottlenose dolphins show stable patterns of association for many years (Wells et al. 1987). This combination of highly structured patterns of association between individuals, coupled with fluid patterns of social grouping, argues that individual specific social relationships are an important element of bottlenose dolphin societies (Tyack 1986a). It is difficult to imagine how dolphins that share a bond could remain together without an individually distinctive acoustic signal. Caldwell and Caldwell (1965) demonstrated that each dolphin within a captive group produced an individually distinctive whistle. The Caldwells called these *signature whistles*, and they postulated that signature whistles function to broadcast individual identity. Initial studies of signature whistles in adult dolphins, primarily of isolated animals, suggested that well over 90 % of an individual's whistle repertoire was made up of its signature whistle (reviewed in Caldwell et al. 1990). Signature whistles were initially discovered in captive dolphins, but similar signature whistles have been documented in wild dolphins (Sayigh et al. 1990). In the wild, it is seldom possible to determine which dolphin makes a whistle when a group is swimming freely, but this can be accomplished by recording dolphins when they are restrained in a net corral. When a dolphin is held in the corral, one can attach a hydrophone to its head with a suction cup. This is not a very natural context for these animals, but it allows one to sample the results of normal whistle development among wild dolphins. Moreover, when dolphins are swimming freely immediately after being corralled, or when they are recorded immediately after release, they produce whistles very similar to those produced while they were restrained (Sayigh et al. 1990). Recordings of whistles from wild dolphins demonstrate that dolphins develop signature whistles by 1 – 2 years of age and these are stable for over a decade.

5.3.2.1
Mother—Infant Recognition

All mammalian young are born dependent upon the mother. Most need to suckle frequently, and many species depend upon the mother for thermoregulation and protection from parasites and predators. Most mammals have a vocal system for regaining contact when mother and offspring are separated. Colonially breeding seals often face difficult mother-young location and recognition problems. In many otariid seals, a mother leaves her young pup on land in a colony of hundreds to thousands of animals, feeds at sea for a day or more, and then must return to find and feed her pup. Among Galapagos fur seals, *Arctocephalus galapagoensis*, pups spend more time calling during their first day of life than later, and mothers learn to recognize the calls of their young within the first day of life (Trillmich 1981). Mothers give pup contact calls as early as during birth. Later, mothers can signal with a pup-attraction call to a pup that is moving away. When a mother returns from feeding at sea, she comes up on the beach giving pup-attraction calls. Her own pup usually seems to recognize her call and approaches. If a pup approaches to suckle, the mother sniffs the pup for a final olfactory check. If it is not her offspring, she almost always rejects the pup, a rejection which can cause injury or occasionally death to the pup (Trillmich 1981). There is thus a strong incentive for both mother and pup to recognize each other correctly. Playback experiments of pup attraction calls indicate that 10-12-day-old pups prefer their mother's call, and this recognition persists until they become independent at more than 2 years of age (Trillmich 1981).

The young of many dolphin and other odontocete species are born into groups comprised of many adult females with their young, and they rely upon a mother-young bond that is even more prolonged than that of otariids. Many of these species have unusually extended parental care. For example, both sperm whales (*Physeter macrocephalus*) and pilot whales (*Globicephala macrorhynchus*) suckle their young for up to 13–15 years (Best 1979; Kasuya and Marsh 1984). Bottlenose dolphin calves typically remain with their mothers for 3–6 years (Wells et al. 1987). These dolphin calves are precocious in locomotory skills, and swim out of sight of the mother within the first few weeks of life (Smolker et al. 1993). Calves this young often associate with animals other than the mother during these separations. This combination of early calf mobility with prolonged dependence would appear to select for a mother-offspring recognition system in bottlenose dolphins. In the following paragraphs and Section 5.3.3, the terms "dolphin", "mother", and "calf" will be used to refer to the bottlenose dolphin, *Tursiops truncatus*.

Dolphin mothers and young use signature whistles as signals for individual recognition. Observations of captive dolphins suggest that whistles function to maintain contact between mothers and young (McBride and Kritzler 1951). When a dolphin mother and her young calf are forcibly separated in the wild, they whistle at high rates (Sayigh et al. 1990); during voluntary separations in the wild, the calf often whistles as it is returning to the mother (Smolker et al. 1993). Experimental playbacks have demonstrated that mothers and offspring respond preferentially to each others' signature whistles even after calves become independent from their mothers (Sayigh 1992).

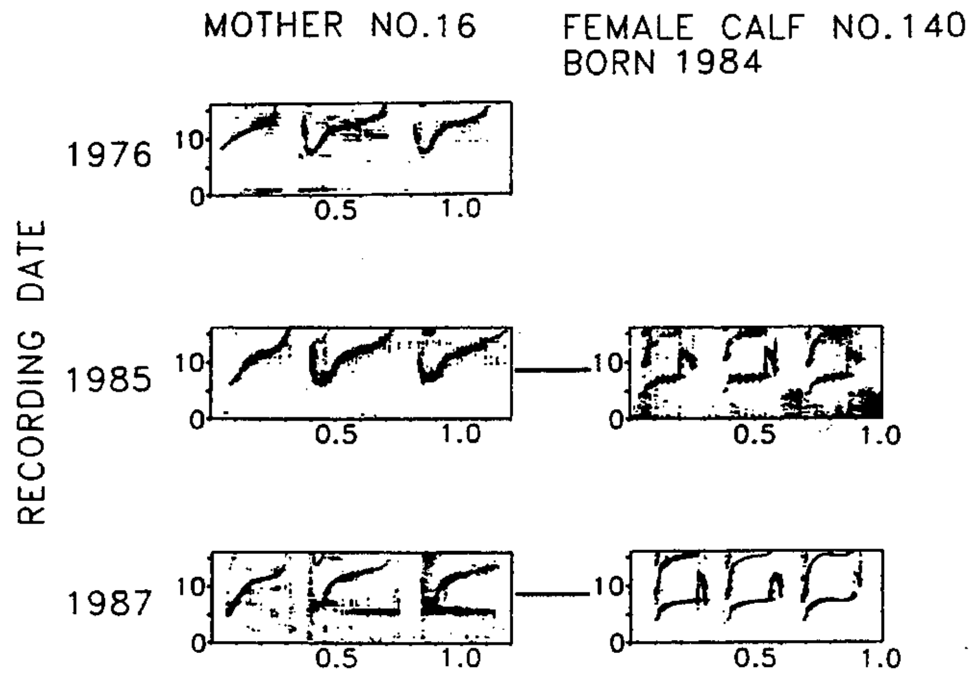

Fig. 9. Spectrograms of signature whistles from one wild adult female bottlenose dolphin recorded over a period of 11 years and of her daughter at 1 and 3 years of age (Reprinted with permission from Fig. 2 in Sayigh et al. 1990). Note the stability of both signature whistles. The *x-axis* indicates time in seconds and the *y-axis* indicates frequency in kilohertz on the spectrogram

Dolphins do not just use whistles for mother–infant recognition. Calves show no reduction in whistling as they wean and separate from their mothers. While adult males are not thought to provide any parental care, they whistle just as much as adult females. Bottlenose dolphins may take up to 2 years to develop an individually distinctive signature whistle, but once a signature whistle is developed, it appears to remain stable for the rest of the animal's lifetime (Figure 9; Caldwell et al. 1990; Sayigh et al. 1990; Sayigh et al. 1995). These results suggest that signature whistles continue to function for individual recognition in older animals.

5.3.3
Vocal Learning Among Marine Mammals

Few animals outside of several families of birds have been shown to modify the acoustic structure of their vocal repertoire based upon what they hear. One source of evidence for vocal learning is imitation of novel sounds. If an animal can imitate a sound that is not normally part of its repertoire, then it learned to modify its normal vocalizations to match the model. Given the lack of evidence for vocal learning among terrestrial nonhuman mammals, there are a surprising number of reports of marine mammals imitating manmade sounds: Hoover, a harbor seal (*Phoca vitulina*) at the New England

Aquarium, imitated human speech well enough to have a recognizable New England accent (Ralls et al. 1985). Captive bottlenose dolphins from many aquaria have been reported to learn to imitate computer-generated tones and pulses. Logosi, a beluga whale at the Vancouver Aquarium, was able to imitate his own name (Eaton 1979). Sperm whales (*Physeter macrocephalus*) have been heard to respond so precisely to a depth sounder that their pulses produce false targets on the depth recorder (Backus and Schevill 1962). These reports include both seals and whales, which have different terrestrial ancestors. Presumably, this means that both groups independently evolved this skill.

Vocal learning may play a particularly important role in the production of individually distinctive calls in marine animals. Many birds and mammals rely upon individually distinctive social relationships within their societies, and many of these species recognize individual differences in the vocalizations of different animals. Slight variations in the vocal tracts of terrestrial animals lead to predictable differences in the voices of individuals. These involuntary characteristics of voice are not likely to be as reliable for diving animals, however. The vocal tract is a gas-filled cavity, and gases halve in volume for every doubling of pressure as an animal dives. Since different parts of the vocal tract are more or less elastic, changes in volume will lead to changes in shape. These depth-induced changes in the vocal tract are likely to outweigh the subtle developmental differences that lead to voice differences. If diving animals rely upon individually distinctive calls, they may need to create them by learning to modify acoustic features under voluntary control, such as the frequency modulation of whistles. This analysis suggests one reason why vocal learning may be more common in marine than terrestrial mammals.

5.3.3.1
Imitation of Signature Whistles

The bottlenose dolphin, *Tursiops truncatus*, is the marine mammal species whose imitative skills are best known. Captive bottlenose dolphins of both sexes are highly skilled at imitating synthetic pulsed sounds and whistles (Caldwell and Caldwell 1972; Herman 1980). Bottlenose dolphins may imitate sounds spontaneously within a few seconds after the first exposure (Herman 1980), or after only a few exposures (Reiss and McCowan 1993). Dolphins can also be trained using food and social reinforcement to imitate manmade whistle-like sounds (Evans 1967; Richards et al. 1984; Sigurdson 1993). The frequency modulated whistle-like sounds that are most commonly used as stimuli for imitation research are similar to signature whistles. My own interest in dolphin whistles was stimulated by the apparent contrast between the evidence that each dolphin tended to produce one individually distinctive whistle and evidence that dolphins were so skilled at imitating manmade whistle-like sounds. Might dolphins be using imitation in their own natural system of communicating by whistles? In order to address this question, it was necessary to develop a method to identify which dolphin makes a sound when animals are interacting together. I have developed several techniques to solve this problem. The first device, called a *vocalight*, is a small hydrophone connected to a display of light-emitting diodes (LEDs) (Tyack 1985). For every doubling of signal intensity (increase of 3 dB), another diode lights up. There are ten LEDs, so the device responds over a range of 30 dB. The vocalight is small and can be attached to a dolphin's head with a suction cup. In order to identify which dolphin produces which whistle, one puts a vocalight with a different color of LEDs on each dolphin. Then one broadcasts underwater sound in air. When one hears a whistle, one looks to see which color of vocalight lit up the most.

A dolphin tends to produce its own signature whistle when it is isolated. However, by using the vocalight, I found that when a captive dolphin is interacting with members of its group, it can also produce precise imitations of the signature whistles of the other dolphins. Imitation of signature whistles is also found in wild dolphins that share strong social bonds (Sayigh et al. 1990), such as mothers and calves or pairs of adult males who may remain together in a coalition for years (Connor et al. 1992).

Studying the function of cognitive skills such as whistle imitation is difficult and often requires both controlled experiments in the laboratory and careful observation in the natural setting in which these skills evolved (Tyack 1993). Experiments on vocal labeling in dolphins demonstrate that dolphins have the cognitive abilities required to use imitated whistles as names. Captive dolphins can be taught to imitate manmade sounds upon command (Richards et al. 1984). In the vocal labeling paradigm, when the trainers gave a dolphin the command to imitate a sound, they would simultaneously play the model sound and hold up an object associated with that sound. For example, for the tune "MARY HAD A LITTLE LAMB", they might show a frisbee, and for "ROW, ROW, ROW YOUR BOAT", they might show a pipe. After the dolphin got used to this, the trainers started occasionally to show the object but not to play the model sound. In order to respond with the right sound, the dolphin had to remember which sound was associated with which object. After sufficient training, the dolphin succeeded in learning how to label each manmade object with an arbitrary manmade tune.

The Richards et al. (1984) vocal labeling experiments suggest that imitated signature whistles might function as similar vocal labels, and that a dolphin may imitate the whistles of particular individuals in order to name them. In order to test whether imitated signature whistles function as names, one must work with a group of three or more dolphins. It is difficult to use the vocalight with groups of more than two animals. When one hears a whistle, one must be able to observe vocalights on all of the animals in the group in order to determine which one lit up the most and therefore which dolphin made the whistle. I therefore developed a small datalogging computer that is also small enough to attach to a dolphin with suction cups (Tyack and Recchia 1991). The computer is mounted in an underwater housing with a hydrophone, preamplifier, and filter. It logs the level and frequency of sound 20 times a second for up to 45 min. As many data loggers as dolphins in the tank are synchronized at the start of a session using a signal from a video time generator. This same generator time-stamps a video recording of the session. A video camera mounted over the dolphin pool provides a video record of behavior, and underwater audio signals from hydrophones in the pool are recorded on hi-fi audio channels of the VCR. Once the session is over, one downloads data from each logger into a personal computer. These data are analyzed after the session using a program that reads data from each data logger. When one finds a time of interest on the videotape, one indicates this time to the program which plots the levels of each data logger and the frequency at the loudest logger. The data logger with the loudest signal is presumed to be on the whistling dolphin.

Neither the vocalight nor the data logger techniques are particularly well suited for use with free-ranging dolphins. Several techniques are currently under development. One scheme is to use a more sophisticated data logger, which can actually record the entire signal of interest. This can either be recovered later or linked to a digital radio telemetry transmitter. Other promising techniques include localizing where sounds are originating using a two-dimensional beamformer or acoustic location system (e.g. Freitag and Tyack 1993) and overlaying the sound source location on an underwater or overhead video image of animals in view.

5.4
Sound Classification

Section 4 on hearing suggests that different species of animal are likely to perceive sounds in different ways. This is due both to differences in receptors and in central auditory processing. For example, timing cues seem more important than frequency in fish, while frequency coding is an important element of mammalian hearing, and mammals are better than fish at frequency discrimination. All good ethologists understand this idea that each animal has its own sensory world. However, when we study animal signals, we initially must rely upon our own senses and instruments to detect and classify them. The development of instruments is particularly important for marine bioacoustics, since we must rely upon electronic detectors and since so many of the signals are outside our own hearing range. The classical approach for analyzing sounds in bioacoustics is to listen to recordings and to perform spectrographic analysis on detected sounds. A sound spectrogram plots the energy of sounds as a function of frequency and time. There is a time window associated with the frequency analysis, and the choice of time and frequency settings has a great impact on what features are apparent and how they appear (Watkins 1967). The way in which spectrographic analysis encodes the energy in different frequencies has some rough analogies to the way in which the cochlea detects energy at frequencies high enough that the auditory system cannot follow the waveform. Spectrograms thus have the advantage that they can present acoustic information in visual figures that may roughly match the way sounds are processed by the peripheral auditory system in mammals (also see discussions by Gerhardt, Clements, and Beeman, this Volume). The humble waveform plot of actual pressure values as a function of time can also be extremely useful, especially for viewing and analyzing temporal features of a signal. This is particularly relevant for those animals which appear to rely primarily on timing features for recognizing conspecific signals. The basic point is that vocalizations should be presented using displays that parallel how the sounds are processed by the auditory system of the species that receives the signal.

When biologists set out to characterize the vocal repertoire of a species or an individual, they typically make lots of recordings, listen to them, and begin to recognize and name classes of signals. Spectrographic analysis can help aid the ear in such recognition, but often the biologist only makes spectrograms of a few examples of each sound type. More detailed data on the repertoire are usually presented as counts of the different signal types. There are several problems and pitfalls with this approach. These will be discussed in the next few paragraphs.

Humans cannot directly sense many features that are easily detected by other animals. We must be careful to use the proper instruments to detect and faithfully record, for example, the high frequency clicks of a porpoise or the low frequency calls of a blue whale (see Pye and Langbauer, this Volume). Studies of visual observations of animal behavior put strong emphasis on avoiding attentional biases and inter-observer reliability (Altmann 1974). Classical bioacoustic analyses are vulnerable to both problems. Humans are excellent at creating categories out of continuous variables and our categories may not match those of the species under study. If we set out to make categories, we may miss graded or continuous elements of a communication system. There are several alternatives to the subjective categorization of sounds. One approach is to measure well-defined acoustic features from a set of sounds and then to analyze them using multivariate statistics. For example, Clark (1982) performed this kind of analysis on the calls of southern right whales, and found that the calls did not fall into the discrete categories suggested by earlier analyses, but formed a structured continuum. Many studies have extracted a few acoustic features such as duration, and minimum and maximum frequency for statistical analysis. These features have been selected for ease of measurement, not necessarily because of their salience to the animals. Measurements of extreme minima and maxima are not very reliable, being modified by signal to noise and spectrographic settings. Modern digital signal processing facilitates making more robust measurements, measuring more features, and selecting features for their relevance to the animals.

A variety of promising signal processing techniques have been developed for the detection and classification of transient signals. Mellinger and Clark (1993) developed a spectrogram correlator filter which compares the spectrogram of a transient signal with a stored spectrographic model, and this had an excellent error rate of only 3.6 % when classifying the endnote from songs of bowhead whales (Potter et al. 1994). Potter et al. (1994) also used *neural net* processing to classify calls of bowhead whales, which decreased the error rate to only 22 out of 1475 calls for a rate of 1.5 %. The neural net has two advantages over the linear detector. The model for the spectrogram filter was synthesized by a human, while the neural net is able to calculate a better spectrogram model using a subsample of the data set for training. The neural net is also better able to reject interfering calls which share features with the desired call.

Another approach for classifying sounds is to make an explicit model of which acoustic features are most salient to an animal. For example, most analyses of signature whistles focus upon specific features such as frequency changes in the fundamental frequency of the whistle rather than upon the entire spectrogram. While the frequencies of spontaneous whistles are relatively stable, the timing of whistles changes by up to 30 % or more (Tyack 1986b). Buck and Tyack (1993) developed a method to compare similarity in frequency contour of whistles while allowing timing to vary by a factor of up to 2. This kind of similarity index makes explicit assumptions that the pattern of frequency change of the fundamental is a critical feature for whistles. These assumptions can be tested by comparing the goodness of fit of the index with responses to naturalistic playbacks or psychophysical tests of how dolphins perceive the similarity of different signals.

All of the methods described above still rely upon the human listener to define what constitutes the unit of analysis for a signal. These decisions can be arbitrary, yet are very important for later conclusions. For example, when people compare whale song with bird song, they are often amazed that whale song can last for over ten minutes while most bird songs last 1 s or so. At first glance, this would seem to indicate that whale song is more complex than bird song. However, the definition of song may differ between whales and birds. When the wren sings AAABBB, we say it is repeating the same song as it moves through its song repertoire. When the whale sings AAABBB, we say it is repeating phrases from theme to theme as it completes its song. I would argue that the appropriate comparison is either between the bird song and the humpback phrase or between the bird's song repertoire and the humpback song. Many birds sing a structured series of songs that may last many minutes. Song bouts in whales and birds can last up to hours, so there may not be a great difference in the durations of the two displays.

The comparison of whale phrases with bird song raises questions about how an outside observer can parse a sequence of animal vocalizations into the appropriate units. An example from human communication will illustrate the point that one cannot analyze sequences of vocalizations without making decisions about the proper signal unit. A critical feature of human speech is the way it is chunked into different levels of organization, from phonemes to words and sentences. While we humans effortlessly parse phonemes in speech, the acoustic boundaries between phonemes are not obvious. In spoken speech, the features of one phoneme may depend upon and leak into the next phoneme, even if these phonemes are from two different words (e.g.,Öhman 1966; see also discussion by Rubin and Vatikiotis-Bateson, this Volume). It has proven very difficult to develop schemes to detect phonemes and words from spectrograms of the speech signal. A major focus of linguistics has been to study the rules by which phonemes and words may be combined to make meaningful utterances. There have been attempts to define this kind of syntactic organization in animal communication, but these usually assume that whole utterances form the proper parallel with the phoneme. We do not really know whether or how animals "chunk" their vocal output.

There is also an important statistical issue concerning the unit of analysis of animal signals. Many statistical analyses of communication signals treat each signal as an independent event. When signals occur in a series, they may be serially dependent. This means that one signal may follow another more often than expected by chance. While this kind of serial correlation can inform us about the structure of signals and interactions, the serial dependence of observations can inflate the sample size for some statistical analyses (Kramer and Schmidhammer 1992).

Both humans and many animals detect graded signals categorically (Harnad 1987), but there is no guarantee that we will draw the perceptual boundaries in the same place as our study animals. Even close relatives of Japanese macaques find it difficult to categorize Japanese macaque calls which are easily discriminated by the species which makes the call (Zoloth et al. 1979). If such close relatives differ in how they process species-specific vocalizations, how much less likely are humans to match the appropriate patterns of distantly related animals living in completely different habitats, such as under the sea? Clearly any human- or computer-generated categorization of vocalizations will need to be validated by testing with the species producing the calls.

In addition, variation in the developmental plasticity of vocalizations will also affect how we interpret the vocal repertoire of a species or an individual. For example, when ethologists start to study a species, they traditionally construct a catalog of species-specific displays. Most research in marine invertebrates or fish suggests that each individual does inherit species-specific display patterns with a structure that is not modifiable through experience to any significant degree. However, we have just seen that marine mammals may learn vocalizations used for individually distinctive or group-specific vocal repertoires. They may even add new vocalizations to their repertoire throughout their lifetime, as in the imitated signature whistles, which raises questions about the applicability of the model of a fixed vocal repertoire.

5.5

Acoustic Localization and Telemetry Open New Windows on Communication Among Marine Animals

A primary obstacle to progress in the study of social communication in marine animals has been the difficulty of identifying which animal within an interacting group produces a sound underwater. Biologists who study terrestrial animals take it for granted that they can identify which animal is vocalizing. They can use their own ears to locate the source of a sound and to direct their gaze. Most terrestrial animals produce a visible motion associated with the coupling of sound energy to the air medium. Mammals and birds open their mouths when vocalizing, many insects produce visible stridulation motions, and frogs inflate their throat sacs. Once their gaze has been directed to the sound source, terrestrial biologists can correlate movements associated with sound production with the sound they hear to confirm which animal is vocalizing. The simplicity of this process should not obscure how important it is for research on communication. Without this ability, researchers can scarcely begin to tease apart the pattern of signal and response that inform us about a system of animal communication.

Humans are not able to locate sounds underwater in the same way they locate airborne sounds. Furthermore, while many fish and invertebrates produce visible motions coordinated with sound production, whales and dolphins seldom do. Some dolphin sounds are coordinated with a visible display, like the so, called "jaw clap" which occurs at the same time as an open mouth display. Dolphins also occasionally emit a stream of bubbles while vocalizing. But these special cases may bias the sample and are not common enough to allow systematic analysis. The need for some technique to identify which cetacean produces which sound during normal social interaction has been discussed for over three decades. The following three different approaches have emerged:

1. An electro-acoustic link between animals isolated in two tanks
2. Passive acoustic location of sound sources using an array of hydrophones
3. Telemetry of information about sound production from each animal in a group

Several investigators have attempted to study communication between isolated captive dolphins using an electronic acoustic link between two pools (Lang and Smith 1965; Burdin et al. 1975; Gish 1979). However, this approach has several serious drawbacks.

The electronic reproduction of dolphin sounds may be discriminably different from natural sound, and it is next to impossible to control for this problem in electronic acoustic link experiments. Even if dolphins accept the acoustic quality of the link, the sounds emanate from an underwater sound projector rather than from another dolphin. As soon as an animal approaches the source and can inspect the projector, it is likely to respond differently than if the source was another dolphin. Furthermore, in order to study the social functions of vocalizations, one would hope to study what roles they play in social interactions. However, the isolated dolphins are able to interact only acoustically.

The second technique, acoustic location of vocalizing animals, is a promising method for identifying which animal is producing a sound. It involves no manipulation of the animals, just placement of hydrophones near them. In some applications, animals may vocalize frequently enough and be sufficiently separated that source location data may suffice to indicate which animal produces a sound. Tracks of continuously vocalizing finback whales, *Balaenoptera physalus*, were obtained in the early 1960s using bottom mounted hydrophones made available to geologists by the US Navy (Patterson and Hamilton 1964; an example of data from these hydrophones is shown in Figure 2). Hydrophones placed on the sea floor to record seismic activity have also been used more recently to track blue and finback whales (McDonald et al. 1995).

The US Navy has devoted considerable resources to using bottom mounted hydrophones in order to locate ships and to track them. These sophisticated systems have recently been used to locate and track whales over long ranges, including one whale tracked for >1700 km over 43 days (Figure 10; Costa 1993). These arrays have proven capable of detecting whales at ranges of hundreds of kilometers, as was predicted by the acoustic models described in Payne and Webb (1971) and Spiesberger and Fristrup (1990). For biologists used to digesting the trickle of information available on the vocalizations of baleen whales, data from these arrays gushes forth as if from a fire hydrant. Thousands of vocalizations may be detected per day, some of them only vaguely similar to sounds identified to species in the earlier literature. One set of problems arises from dealing with this volume of data, but problems just as serious remain with keeping the analysis rooted in basic biological questions. Early studies of whale vocalizations were plagued by the potential confusion that a sound recorded in the presence of one species might be produced by an animal of another species just over the horizon or under the water. Ground truthing of species identification is critical for much of these data, and questions will remain about new sounds not compared with a visual record, for one must compare the source location with a visual record of the animal's locations in order to identify which animal produces a sound.

Several different approaches have been used to locate the sounds of animals over shorter ranges from locations where one could look for the vocalizing animal(s). Watkins and Schevill (1972) devised a four hydrophone array that could rapidly be deployed from a ship. This array has been used to locate vocalizing finback whales, right whales (*Eubalaena glacialis*), sperm whales (*Physeter macrocephalus*), and several species of dolphins. This array is not rigid, and the hydrophone locations must be calibrated using underwater noise sources called pingers. When the array was first used near sperm whales, the pingers were low enough in frequency to be detected by the whales, which immediately stopped vocalizing, reducing the value of the array (Watkins and Schevill

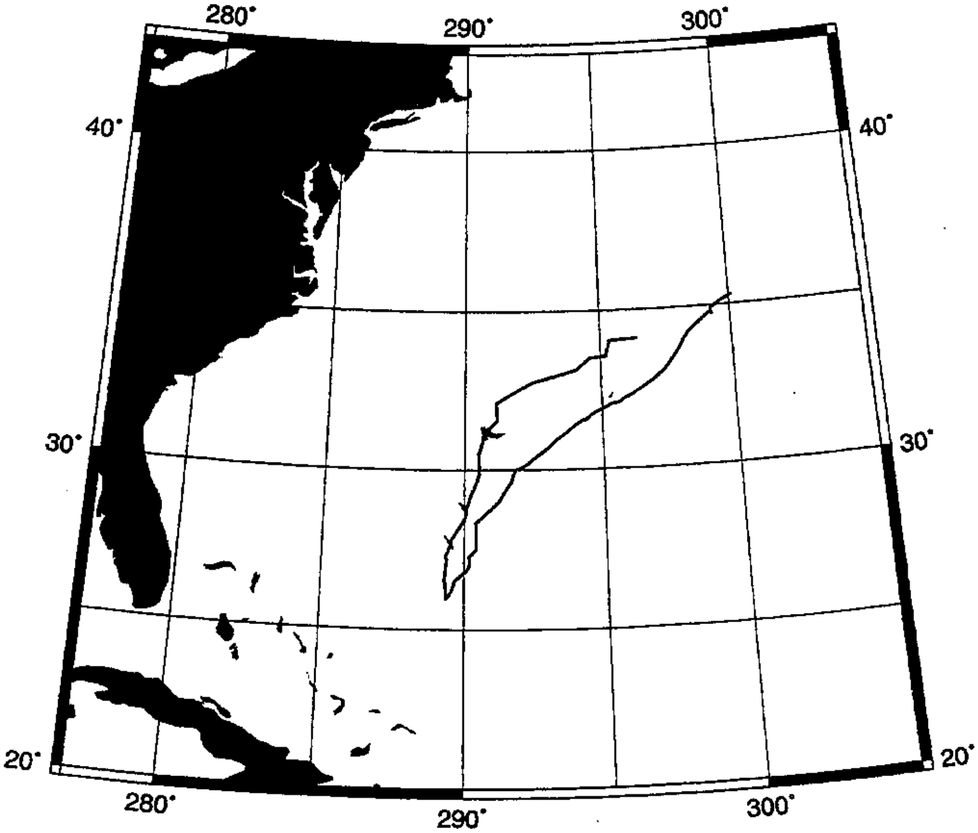

Fig. 10. Track of vocalizing blue whale, *Balaenoptera musculus*, made using the US Navy's Sound Surveillance System (SOSUS) arrays. (Courtesy of Christopher Clark, Laboratory of Ornithology, Cornell University)

1975). Since that time, the array has been deployed with higher frequency pingers and has provided important data on the coda repertoires of individual sperm whales and coda exchanges between different sperm whales (Watkins and Schevill 1977). The array has not been so useful for identifying which dolphin produces a sound (Watkins and Schevill 1974). These animals move rapidly and often swim so close to one another that source locations are not enough by themselves to identify which animal produces a sound. Locations are only calculated back in the laboratory, and it has proved difficult to record the location of different individuals in sufficient detail to allow correlation with the acoustic source locations. Freitag and Tyack (1993) present a different approach to locating dolphin sounds, but in this application it was also difficult to relate acoustic locations to visual records of animal locations. Clark (1980) developed a device that measures the phase difference for a vocalization of a southern right whale (*Eubalaena australis*) arriving at different hydrophones in a relatively small rigid array. This device gives source bearings in real-time and was deployed just off a coastal observation site where it was used successfully to correlate right whale sounds and behavior. Clark et al. (1986) have used a computer in the field to obtain real-time source locations of vocalizing bowhead whales (*Balaena mysticetus*), but it also proved difficult to associate visual sightings with acoustic source locations in this study.

The third technique does not require locating each animal within a group. If each animal carries a telemetry device which records or transmits acoustic data while on the animal, then the repertoires of each individual can be determined. The biggest problem for telemetry has been deciding how to transmit the information effectively without disturbing the animals. Evans and Sutherland (1963) proposed the development of a radio telemetry device to broadcast sounds from a dolphin's head. This technique is limited to applications where the antenna remains above water, for the conductivity of seawater limits electromagnetic transmission, with losses increasing with frequency (Mackay 1968). The use of sound for underwater telemetry is common, since sound has favorable propagation characteristics underwater. Sonic telemetry tags have proved extremely valuable for tracking fish, seals, and some whales (e.g., Amlaner and MacDonald 1980). However, there are serious limitations to the use of sonic telemetry with dolphins and possibly other cetaceans. If the sounds of the telemetry device are audible to the animal, they may interfere with normal behavior. Many species of dolphin can hear frequencies as high as 150 kHz. Frequencies higher than this attenuate so rapidly in sea-water that they are not particularly effective for sonic telemetry (Table 1). These problems with telemetry have led biologists to develop recoverable tags that record data while on an animal, but that need to be recovered from the animal in order to download the data. Recently, biologists have had successful programs recovering such tags from seals, porpoises, and baleen whales. Recoverable acoustic tags may have scientific uses well beyond identifying vocalizations. Figure 11 shows acoustic and dive data sampled from an elephant seal as it swam in Monterey Bay. The tag was able to monitor both the acoustic stimuli heard by the seal and the acoustic signatures of the seal's breathing and heart beat.

6

Acoustic Impact of Human Activities on Marine Animals

Since marine mammals and humans both produce and use sound underwater, there is potential competition for channel space (Green et al. 1994). Transient sounds of biological origin may dominate the noise for manmade sonars in some regions (Urick 1983). Taking the animals' point of view, Payne and Webb (1971) have raised concerns about the potential masking effects of shipping noise on whale communication. Sound generated by commercial shipping is the dominant source of underwater noise over the entire globe in the frequency range from about 20 to 500 Hz, elevating the average ambient by tens of dB (Figure 12; Urick 1983). Judging by the similar frequency range of vocalizations of baleen whales, baleen whales are likely to be sensitive at these frequencies. This is also the primary range of hearing in most marine fish (Figure 5). Myrberg (1980) points out that noise from rough seas or shipping traffic may reduce the effective range of the courtship chirps of bicolor damselfish from 9 m at sea state 1 with light shipping traffic to only 1 m when shipping traffic is heavy. This carries the potential

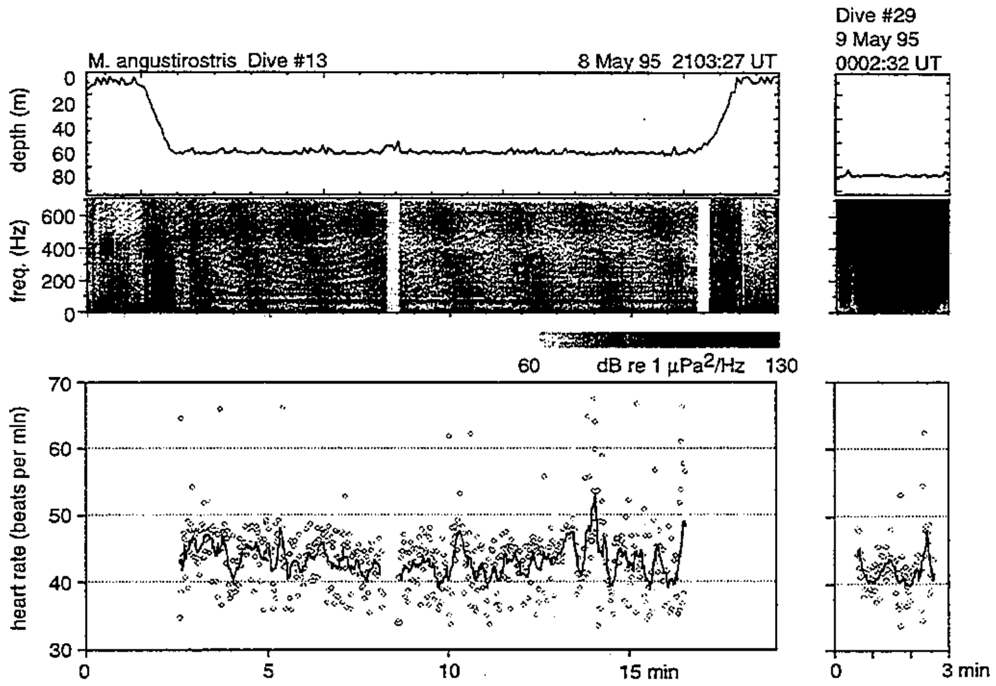

Fig. 11. Data recorded from tag deployed on an elephant seal. *Mirounga angustirostris*, as it swam across Monterey Bay, California. *Top* Depth of seals dive measured with a pressure sensor. *Middle* Spectrogram of noise sensed from a hydrophone on tag during this dive. Darker gray represents higher noise levels as indicated on the horizontal gray scale bar; breathing noises made by seal at surface (*dark areas* below 200 Hz at start of record); flow noise from rapid swimming as seal starts its descent (*broader frequency band of dark gray*). As soon as seal reaches bottom of its dive at nearly 60 m, flow noise is greatly reduced; noise from ship passing overhead of seal (*middle curved bands of light and dark gray*); data gaps as tag was writing data from memory to a disk drive (two *narrow white vertical lines*). Acoustic record from seal was also able to detect low frequency sounds of its heart beat. *Bottom* Estimates of heart rate of diving seal made from detecting this acoustic signature of heart beat. (Courtesy of William Burgess, Monterey Bay Aquarium Research Institute)

for disrupting reproductive activity. Environmental noise has been shown not only to mask communication signals, but also to cause physiological stress responses, hearing loss, and interference with normal activities in humans and other terrestrial animals.

Little attention has focussed upon the impact of noise on marine invertebrates or fish, but some research has focused upon endangered species and marine mammals because of the greater legal protection they enjoy under United States law. For example, since lease of offshore areas for oil exploration and production requires environmental impact statements in the USA, the federal Minerals Management Service has funded a number of studies attempting to quantify the effects of noise that results from oil industry activities. More is known about whale responses to these stimuli than to any other human noise source. For example, one sound playback study involved observation of > 3500 migrating gray whales, *Eschrichtius robustus*, and showed statistically significant responses to playback of industrial noise (Malme et al. 1984). These whales were tracked from elevated shore observation sites using the same theodolite method described for singing humpbacks. This is one of few ways to observe whales without

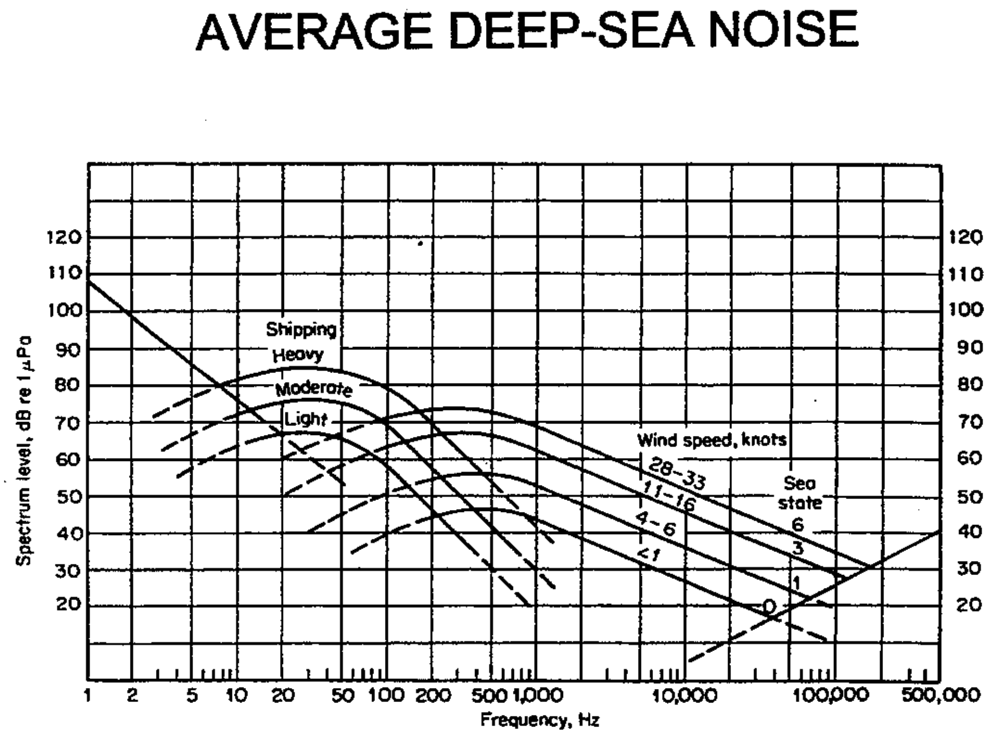

Fig. 12. Average deep-sea noise levels. Noise below about 20 Hz primarily stems from geological activity. Shipping noise dominates the ambient noise from 20 to 200 Hz. Above this frequency, noise stems primarily from wind and waves. (from Urick 1983, used with permission)

having to worry about whether the observation platform might be altering the animals' behavior. Whales slowed down and started altering their course away from the sound source at ranges of 1–3 km, where the estimated level of the playback source was near the local ambient noise level. This resulted in an avoidance reaction — an increase in the distance between the whales and the source at their closest point of approach (Figure 13). Half of the migrating gray whales avoided exposure to the continuous playback stimuli at received levels ≥ 117–123 dB re 1 μPa. The 50 % avoidance level for airgun pulses used in seismic surveys was 170 dB. The ranges predicted for a 50 % probability of avoidance were 1.1 km for one of the continuous playback stimuli, a drillship, and 2.5 km for the seismic array.

There is little reason to expect that oil industry activities are more likely to harm whales than other activities. The acoustic impacts of the oil industry upon whales have been highlighted primarily for political reasons, such as federal government involvement in leasing offshore tracts to the oil industry. Other human activities, such as ships, underwater explosions, military sonar, and acoustic tomography may generate enough noise to have similar potential impacts. These impacts may be particularly important if they inhibit the recovery of marine mammal populations which were depleted in the past by human hunting or whaling. Humans may have to be more careful now than in the past to avoid polluting the habitat of wild animals by noise as well as chemical contaminants. Unfortunately, we know very little about what effect noise has on the hearing and behavior of most marine species. Even for well-studied species, it is unwise to extrapolate to contexts beyond those studied. For example, the migrating gray whales were watched as they were exposed to a novel and relatively faint source. They might not show the same avoidance response to a more distant and louder source after they habituated to repeated exposure.

In order to protect humans against exposure to noise in the workplace, the US government pays little attention to annoyance or behavioral disturbance, but instead focuses on preventing hearing loss (EPA 1974). Safe levels of noise are determined in experiments where the hearing of a subject is tested before and after exposure to a well-defined noise source. When the level and duration of the noise exposure is just enough to yield a detectable decrement in hearing ability, this is called a *temporary threshold shift* (TTS) for hearing. While this TTS does no harm in itself, it is assumed that chronic repeated exposure to levels that cause TTS are likely to lead to permanent hearing loss. Therefore, regulations limit exposure to sound beyond the levels and durations that cause TTS. So many marine animals depend so heavily on sound that there is reason to be concerned that permanent hearing loss might affect biologically significant activities. Ideally one might want to define standards for exposure to underwater noise in order to prevent a negative impact, particularly on the recovery of endangered marine animal populations. Unfortunately there is not one marine animal for which we can specify that a specific noise exposure leads to hearing loss. Furthermore, noise might disrupt biologically significant activities of animals at levels lower than those required to cause hearing loss. Until both hearing loss and behavioral disruption are better defined, it will not be possible to regulate noise exposure in a way that protects marine animals while minimizing the burden on human seagoing activities. Marine bioacoustics thus clearly is not just a fascinating area of basic scientific research, but also is central to protecting our marine environment from habitat degradation by noise pollution.

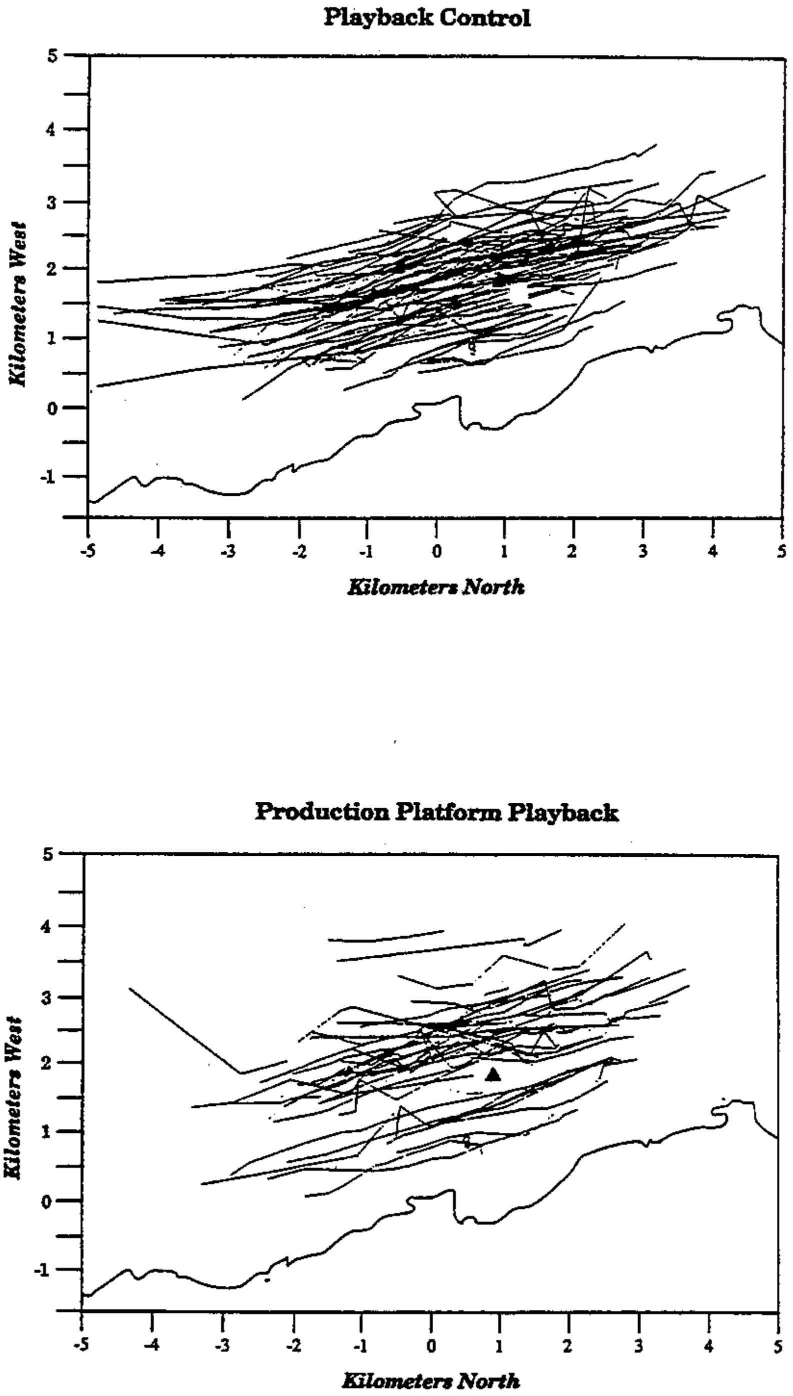

Fig. 13. Plot of tracks of migrating gray whales during control observations (*top*) and during playback of the noise of an offshore oil industry production platform (*bottom*). The *black triangle* at approximately 1 km north and 2 km west marks the location of the playback vessel. (Adapted from Malme et al. 1984, with permission)

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