Pelagic larvae Larvae of marine animals that swim freely in the water column.

Planktotrophic larvae Pelagic larvae of marine animals that develop freely in the surface waters of the ocean, feeding on planktonic organisms.

Selective deposit feeders Animals feeding on surface particles of organic matter or sediment particles supporting a rich bacterial flora.

Suspension feeders Animals feeding on organisms or organic detritus suspended in the water column.

Viviparity Young are born fully developed either from eggs retained within the body of the mother (oviparity) or after internal embryonic development.

See also

Benthic Boundary Layer Effects. Benthic Foraminifera. Deep-sea Fauna. Demersal Fishes. Demersal Species Fisheries. Grabs for Shelf Benthic Sampling. Macrobenthos. Meiobenthos. Microphytobenthos. Network Analysis of Food Webs. Phytobenthos. Tides.

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BIOACOUSTICS

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Introduction

The term ‘bioacoustics’ has two different usages in ocean sciences. Biological oceanographers use active sonars to map organisms in the sea. Since they use sound to detect marine life, they often call this approach ‘bioacoustics’. The other sense of bioacoustics involves studying how animals use sound themselves in the ocean. This is the kind of bioacoustics covered in this article.

Humans are visual animals, and we think of vision as a primary distance sense because light carries so well in terrestrial environments. However, light is useful for vision under the sea only over ranges of tens of meters at best. Sound, on the other hand, propagates extremely well in water – that is why oceanographers so often select sound as a medium for exploring the sea or for communicating under the sea. Sound propagates so well under water that a depth charge exploded off Australia can be heard in Bermuda. Just as we can hear well but emphasize vision, so many marine mammal species see well but emphasize hearing. It is possible to gauge the relative importance of audition versus vision in animals by comparing the number of nerve fibers in the auditory versus the optic nerves. Of all marine mammals, the cetaceans are the most specialized to use sound. Most cetaceans have auditory:optic ratios of fiber counts that are 2–3 times those of land mammals, suggesting that audition is more important than vision. Some cetaceans also use sound to echolocate. Dolphins have a large repertoire of vocalizations spanning frequencies from below 100 Hz to over 100 kHz, and dolphins have evolved high-frequency echolocation similar to some human-made sonars and to the biosonar used by bats.

Marine mammals not only hear well, they are also very vocal animals. The sounds of marine mammals are now well known, but the first recordings identified from a marine mammal species were only made in the late 1940s. In the 1950s and 1960s, there was rapid growth in studies of how dolphins echolocate using high-frequency click sounds and of field studies associating different sounds with different species of marine mammal. Marine mammal bioacoustics during this period was concerned primarily with identifying which species produced which sounds heard under water. Much of this research was funded by naval research organizations because biological sources of noise can interfere with military use of sound in the sea.

Elementary Acoustics

Sound consists of mechanical vibrations that propagate through a medium. Sound induces movements or displacements of the particles in the medium. Imagine a small sphere that expands to create a denser area. This compression will propagate as particles are displaced in the direction of propagation. If the sphere then contracts, it can create an area of rarefaction, or lower density, and this also can propagate outward. These compressions or rarefactions can be expressed in terms of particle displacement or as a pressure differential.

Now imagine a sound source that creates a series of compressions and rarefactions that propagate through the medium. A source with a purely sinusoidal pattern of compression and rarefaction would produce energy at only one frequency. The frequency of this sound is measured in cycles per second. A sound that takes t seconds to make a full cycle has a frequency $f = t^{-1}$. Older references may refer to frequency in cycles per second, but the modern unit of frequency is the Hertz (Hz) and a frequency of 1000 Hz is expressed as one kiloHertz (1 kHz). If a sound took 1 s for a full cycle, it would have a frequency of 1 Hz. The wavelength of a tonal sound is the distance from one measurement of the maximum pressure to the next maximum. The speed of sound is approximately $1500\,\mathrm{m\,s^{-1}}$ in water, roughly five times the value in air, $340\,\mathrm{m\,s^{-1}}$. The speed of a sound c is related in a simple way to the frequency f and the wavelength λ by $c = \lambda f$. An under-water sound with $f = 1$ Hz would have $\lambda = 1500$ m; for $f = 1500$ Hz, $\lambda = 1$ m. Not all sounds have energy limited to one frequency. Sounds that have energy in a range of frequencies, say in the frequency range between 2000 and 3000 Hz (2 and 3 kHz), would be described as having a bandwidth of 1 kHz.

One can imagine a sound wave as a growing sphere propagating outward from a compression or rarefaction generated by a point source. The initial movement of the source will have transmitted a certain amount of energy to the medium. If none of this energy is lost as the sound propagates, then it will be evenly diluted over the growing sphere. The acoustic intensity is defined as the amount of energy flowing through an area over a unit of time. As the sphere increases in radius from 1 to r, the surface area increases to $4\pi r^2$. The intensity of a sound thus declines as the inverse of the square of the range from the source (r^{-2}). A sound in the middle of the ocean can be thought of as spreading in this way until it encounters a boundary such as the surface or seafloor that might cause reflection, or an inhomogeneity in the medium that might cause refraction. One fascinating acoustic feature of the deep ocean is that sound rays propagating upward may refract downward as they encounter warmer water near the surface, and downward-propagating rays will refract upward as they encounter denser water at depth. When one is far from a sound source compared to 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 intensity would decline as the inverse of the first power of the range, or r^{-1}. This involves much lower loss than the inverse square spreading loss in an unbounded medium.

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 per unit distance, but this constant is dependent upon signal frequency. 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. A 100 Hz sound can travel over a whole ocean basin with little absorption loss, while a 100 kHz sound would lose half its energy just traveling about 100 m.

Relating Acoustic Structure to Biological Function of Marine Mammal Calls

Understanding the physics of sound in the sea can help us understand why animals make the kinds of sound they do. For example, the calls of baleen whales are low-frequency because they are adapted for long-range propagation in the deep sea. Large baleen whales have evolved abilities to produce and to hear low-frequency calls well-suited for long-range communication. Blue whales and fin whales produce the lowest-frequency signals of all marine mammals, so low that humans can barely hear them. The long moans of blue whales, *Balaenoptera musculus*, have fundamental frequencies in the 14–36 Hz band and they last several tens of seconds. The pulses of finback whales, *Balaenoptera*

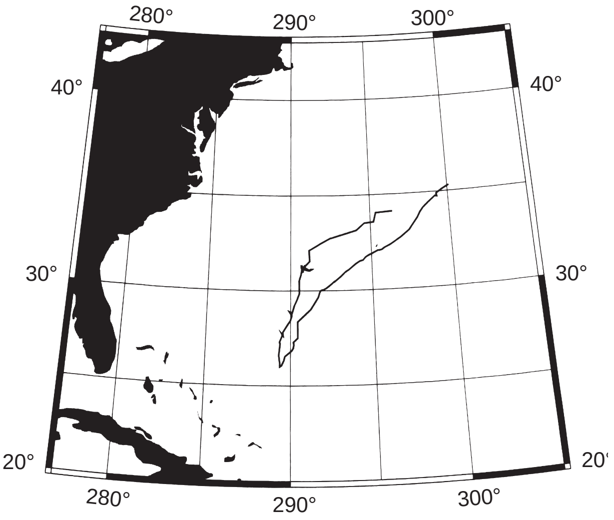

Figure 1 Track of a calling blue whale, *Balaenoptera musculus*, as it swam 1700 km over 43 days. The whale was tracked using the Integrated Underwater Sound Surveillance System (IUSS) of the US Navy. (From Figure 4.17 of Au *et al*. (2000).)

physalus, range roughly between 15 and 30 Hz and last on the order of 1 s. Particularly during the breeding season in mid-latitudes, finbacks produce series of pulses in a regularly repeating pattern in bouts that may last many days.

These loud low-frequency sounds appear to be specialized for long-range propagation in the sea. Absorption is negligible at the frequencies of these sounds. While acoustic models predicted that these sounds could be detected at ranges of hundreds of kilometers, it is only recently that this has been confirmed empirically. During the Cold War, the US Navy developed bottom-mounted hydrophones to locate ships and to track them. After the end of the Cold War, these sophisticated systems were made available to biologists, who have worked with Navy personnel to locate and track whales over long ranges, including one whale tracked for more than 1700 km over 43 days (**Figure 1**). These arrays have proven capable of detecting whales at ranges of hundreds to thousands of kilometers, as was predicted by the earlier acoustic models.

The physics of sound can also help explain why dolphins specialize in high-frequency sounds. Dolphins can detect distant objects acoustically by producing loud clicks and then listening for echoes. The clicks used by dolphins for echolocation have been well described. The echolocation clicks of bottlenose dolphins are very short (<100 μs), with a rapid rise-time and a relatively broad bandwidth from several tens of kilohertz up to near 150 kHz (**Figure 2A**). Captive dolphins in a reverberant pool make clicks that are less loud and lower in frequency than dolphins working on long-range echolocation in an open bay. The high-frequency components of these clicks are highly directional. If one moves 10 degrees off the axis of the beam, the click energy is halved and the click contains energy at lower frequencies (**Figure 2B**). The detection abilities of echolocating dolphins are truly remarkable. For example, trained bottlenose dolphins can detect a 2.54 cm solid steel sphere at 72 m, nearly a football field away.

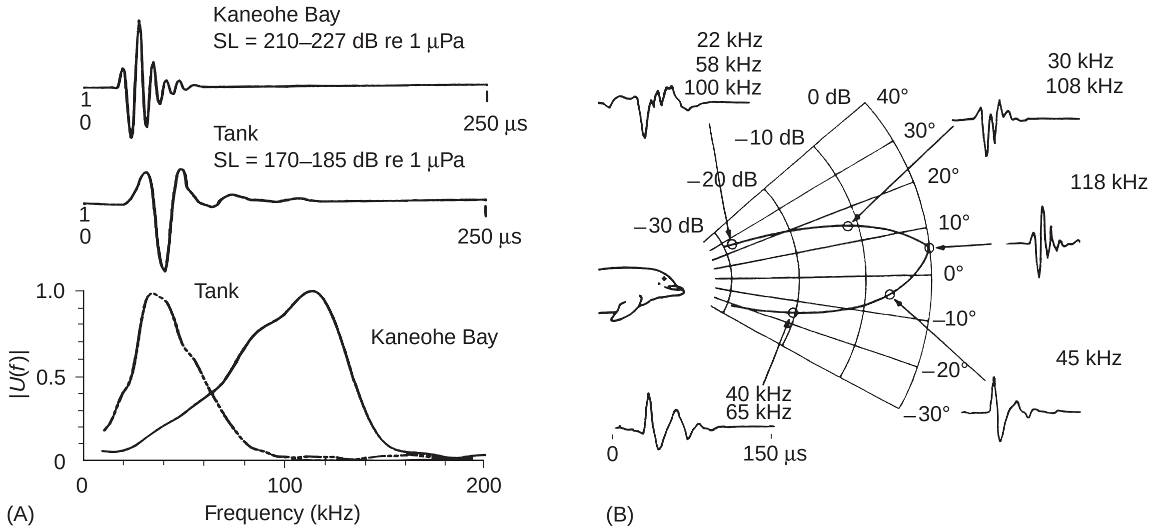

Figure 2 (A) Waveform and spectrum of echolocation clicks of bottlenose dolphins, *Tursiops truncatus*, in open ocean (Kaneohe Bay) and in a tank. The spectrum of the click from the tank (indicated with a dashed line) has a lower frequency peak at 40 kHz. (B) Beam pattern of *Tursiops* echolocation clicks. (μPa = micropascal, reference for sound pressure measurements. SL = source level.) ((A) from Figure 9.1, (B) from Figure 9.5 of Au *et al*. (2000).)

The optimal frequency of a sound used for echolocation depends upon the size of the expected target. Absorption imposes a penalty for higher frequencies, but small targets can best be detected by short-wavelength, or high-frequency, signals. In the nineteenth century, Lord Rayleigh solved the frequency dependence of sound scattering from rigid spherical targets; this is called Rayleigh scattering. A spherical target of radius r reflects maximum energy when the wavelength of the sound impinging on it equals the circumference of the sphere, or when $\lambda = 2\pi r$. The echo strength drops off rapidly from signals with wavelength $\lambda > 2\pi r$. Since $\lambda = c/f$, one can equate the two λ terms to get $c/f = 2\pi r$. The relationship $f = c/2\pi r$ can be found by rearranging terms 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 strong decrease in effectiveness with decreasing frequency. A dolphin echolocating on rigid targets with a 'radius' of 0.5 cm should use a frequency $f \geq c/2\pi r = 1500/(2\pi \times 0.005) \sim 50$ kHz. This is within the frequency range of dolphin echolocation clicks, which include energy up to about 150 kHz. This upper frequency is appropriate for detecting spherical targets with radii as small as 1.5 mm. The hearing of dolphins is also most sensitive at frequencies of roughly 50–100 kHz. If dolphins have a need to echolocate on rigid targets with sizes in the 1 cm range, that helps explain why their echolocation system emphasizes these high frequencies.

Marine Mammal Hearing

In order to detect sound, animals require a receptor that can transduce the forces of particle motion or pressure changes into neural signals. Most mechanoreceptors in animals involve cells with hairlike cilia on their surfaces. As these cilia move, the electric potential between the inside and the outside of the receptor cells changes, and this potential difference modifies the rate of nerve impulses that signal other parts of the nervous system.

Terrestrial mammals evolved an ear that is divided into three sections: the outer, middle, and inner ear. The outer ear and middle ear function in terrestrial mammals to transduce airborne sound into vibrations of a fluid in the inner ear of mammals which contains the cochlea, 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. Sensory cells at different 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 also have varying adaptations for listening under water as opposed to in air. All marine mammals other than sirenians, the sea otter, and cetaceans spend critical parts of their lives on land or ice and some phocid seals communicate both in air and under water. The relative importance of hearing in air and under water has been compared for three pinniped species whose hearing has been tested in both environments. The California sea lion (*Zalophus californianus*) is adapted to hear best in air; the harbor seal (*Phoca vitulina*) can hear equally well in air and under water; and the northern elephant seal (*Mirounga angustirostris*) has an auditory system adapted for under water sensitivity at the expense of aerial hearing.

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. No such matching is required for an animal living in the water, and cetaceans, which are adapted exclusively for listening under water, 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 that is isolated from the skull. High-frequency sound is thought to enter the dolphin head through a thin section of bone in the lower jaw and is conducted to the inner ear via fatty tissue that acts as a waveguide.

Hearing abilities have been tested for those species of marine mammals that can be held in captivity. **Figure 3** shows audiograms from a dolphin, a porpoise, and several pinnipeds. As discussed above, dolphins have hearing specialized to hear very high frequencies up to ten times the upper limit of human hearing. Seals have less acute hearing than do dolphins and they are less able to hear the highest frequencies. 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

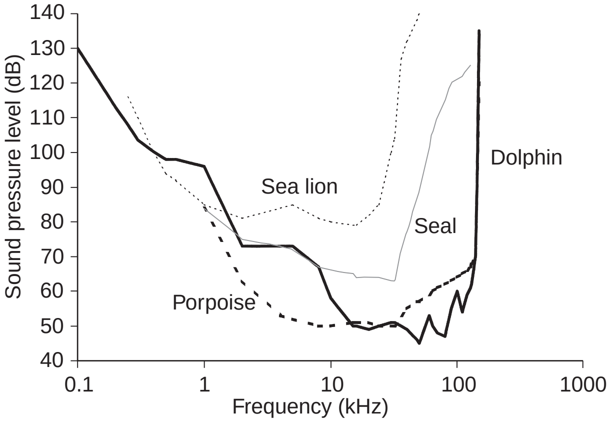

Figure 3 Audiograms from a variety of marine mammals: dolphin *Tursiops truncatus*; porpoise *Phocoena phocoena*; sea lion *Zalophus californianus*; seal *Phoca vitulina.*

their cochlea suggest they are specialized for low-frequency hearing.

Mammalian hearing is designed to analyze the frequency content of sound. Among mammals, dolphins have extraordinarily good abilities of discriminating different frequencies. They can detect a change of as little as 0.2% in frequency, which is close to the resolution of human hearing.

Vocalizations of Marine Mammals

When terrestrial carnivores and ungulates invaded the sea, they encountered new constraints and opportunities for sensing signals. The sirenians, cetaceans, phocid seals, and the walrus (*Odobenus rosmarus*) evolved specializations for using sound to communicate under water and to explore the marine environment; other taxa, including the otariid pinnipeds, sea otter (*Enhydra lutra*) and polar bear (*Ursus maritimus*), vocalize mainly in air. As with hearing, cetaceans show the most elaborate and extreme specializations for acoustic communication under water.

The best-known acoustic displays of marine mammals are the reproductive advertisement displays called songs. The songs of humpback whales are the best known advertisement display in the cetaceans, but bowhead whales also sing. 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 songs of bearded seals, *Erignathus barbatus*, are produced by sexually mature adult males and are heard most frequently during the peak of the breeding season. Male walruses, *Odobenus rosmarus*, also produce complex visual and acoustic displays near herds of females during their breeding season. They use their lips to whistle, and also produce loud sounds of breathing that are audible in air when they surface during these displays. When they dive, displaying males produce a series of pulses under water followed by bell-like sounds. Antarctic Weddell seal males repeat under water trills (rapid alternations of notes) during the breeding season.

Marine mammals also produce a broad variety of displays, including threat displays and recognition displays used for individual or group recognition.

Mechanisms of Sound Production

Most terrestrial mammals produce vocal sounds by vibrating vocal cords in the larynx. It is thought that the polar bear and most pinnipeds make sounds using similar mechanisms. Some adaptations for diving may affect vocalization mechanisms in pinnipeds. Pinnipeds have a more flexible trachea than do terrestrial mammals, so that air inside can compress during a dive, and they have a wider trachea to allow higher rates of air flow. Most pinnipeds can vocalize under water without emitting bubbles; some species have sacs attached to the trachea or upper respiratory sac, but the role of these in vocalization has not been determined. Walruses have many ways of producing sounds. They produce gonglike impulse sounds using specialized pharyngeal sacs, and can even use their lips to whistle in air.

Odontocetes have well developed vocal folds in the larynx, but most biologists argue that odontocetes produce sounds as air flows past the nasal plugs or phonic lips in the upper nasal passages (**Figure 4A**). Mechanisms for sound production must also match the acoustic impedance to the medium of air or sea water, and they may function to direct some sounds in a beam. The beam pattern of dolphin clicks (shown in **Figure 2B**) stems from a complex interaction of reflection from the skull and air sacs, coupled with refraction in soft tissues (**Figure 4A**).

There is a more detailed model of sound production for sperm whales (*Physeter macrocephalus*) than for other cetacean species. Sperm whales have a large organ called the spermaceti organ, which lies dorsal and anterior to the skull (**Figure 4B**). Below the spermaceti organ is the 'junk', which is composed of a series of fatty structures separated by dense connective tissue. The primary vocalizations of sperm whales are distinctive clicks comprising a burst of pulses with equally spaced interpulse intervals (IPIs). Bioacousticians suggest that these

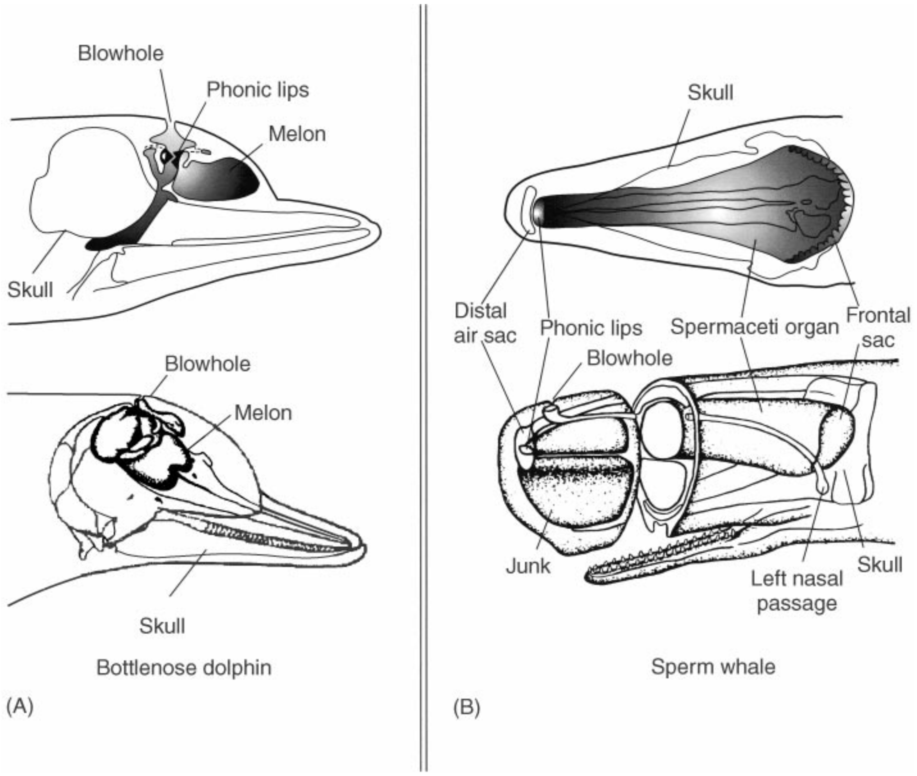

Figure 4 Functional anatomy of sound production in two odontocete cetaceans: (A) bottlenose dolphin *Tursiops truncatus*; (B) sperm whale *Physeter macrocephalus.* (Adapted from Figures 1.4 and 3.1 of Au *et al.* (2000).)

regular IPIs may result from reverberation within the spermaceti organ. The frontal sac at the posterior end of the spermaceti organ has been suggested as a potential reflector of sound and the distal sac as a partial reflector of sound at the anterior end (**Figure 4B**). The source of the sound energy in the click is thought to come from a strong valve (phonic lips) in the right nasal passage at the anterior end of the spermaceti organ (**Figure 4B**). This sound production model suggests that some of the energy from the first pulse within the click is transmitted directly into the water. The remaining pulses are hypothesized to occur as some of the sound energy passes through the anterior reflector into the ocean at each reflection there.

Methods for Bioacoustic Research

It has been difficult to integrate visual observation of social behavior with patterns of vocalization in submerged mammals because it is difficult to identify which animal within an interacting group produces a sound under water. Biologists studying terrestrial animals take it for granted that they can identify which animal is vocalizing by using their own ears to locate the source of a sound and then looking for movements associated with sound production. Humans cannot locate sounds under water in the same way that they locate airborne sounds. Furthermore, marine mammals seldom produce visible motions coordinated with sound production under water. It is even more difficult to attempt behavioral observations on marine mammals during a dive when they are out of sight. The need for some technique to track behavior during a dive and to identify which cetacean produces which sound during normal social interaction has been discussed for over three decades. Two different approaches have emerged: (1) passive acoustic location of sound sources using an array of hydrophones; (2) recording information about behavior and sound production by attaching a tag onto the animal.

Acoustic location of vocalizing animals is a useful method for identifying which animal is producing a sound. It involves no manipulation of the animals, merely 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 and blue whales have been made using bottom-mounted hydrophones. **Figure 1** shows a

1700 km track of a blue whale that was tracked in the early 1990s by US Navy personnel using arrays of hydrophones initially developed to track submarines. Bottom-mounted recording devices are proving cheaper alternatives for biologists today.

Bioacousticians have also developed smaller, portable hydrophone arrays that can be deployed rapidly from a ship or from shore. These arrays have been used to locate vocalizing finback whales, right whales (*Eubalaena glacialis*), sperm whales, and several species of dolphins. Vertical hydrophone arrays can in some settings be used to calculate the range and depth of vocalizing whales. One classic configuration involves a linear horizontal array of hydrophones that is towed behind a ship. Signal processing techniques allow one to determine what bearing a sound is coming from, and to reconstruct the signal from that bearing. Bioacousticians are only just beginning to explore how to use these techniques in behavioral studies of whales.

The second technique does not require locating each animal within a group. If an animal carries a telemetry device that transmits acoustic data recorded at the animal, then the device can record all vocalizations of the animals along with most everything else it hears. This kind of tag can also record depth of dive, movement and orientation of the tagged animal. However, it is difficult to telemeter information through sea water, and marine mammals might sense many of the signals one might want to use for telemetry. 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 for the data to be downloaded. Recently, biologists have had successful programs recovering such tags from many different kinds of marine mammal. Recoverable acoustic tags may have scientific uses well beyond identifying vocalizations. **Figure 5** shows acoustic and dive data sampled from an elephant seal. The tag was able to monitor both the acoustic stimuli heard by the whale, and orientation sensors monitored not just the depth of the dive but also movement patterns such as the fluke beat and physiological parameters such as heart rate. This information is useful to determine reactions of marine mammals to man-made noise, an issue of growing concern.

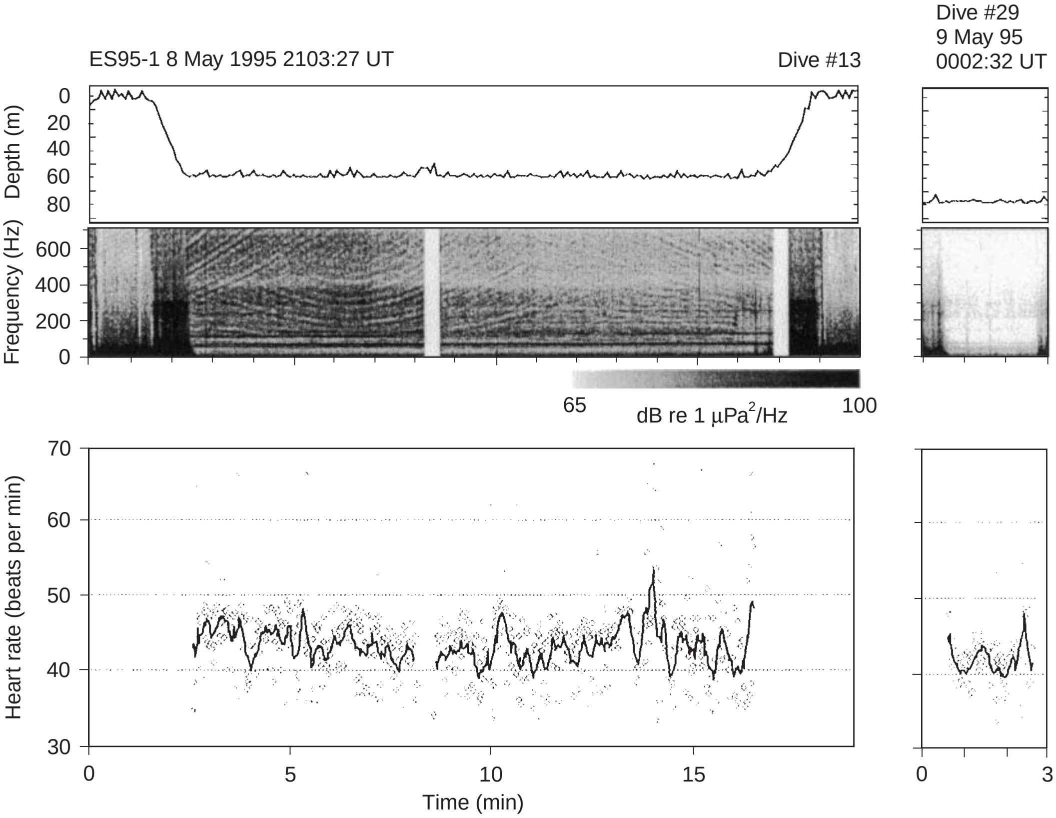

Figure 5 Data on dive profile, acoustic record, and acoustically determined heart rate from a tag on an elephant seal. The acoustic record shows a vessel passing. The closest point of approach occurs at the minimum frequency of the 'U' shaped pattern in the spectrogram at about 6 min. The heart rate differs little from the surrounding times or from a quiet period in a later dive from the same seal. (μPa = micropascal, reference for sound pressure measurements.) (Adapted from Figure 8 of Burgess *et al.* (1998).)

See also

Acoustics, Deep Ocean. Acoustic Scattering by Marine Organisms. Baleen Whales. Marine Mammal Social Organization and Communication. Seals. Sea Otters Sirenians. Sonar Systems. Sperm Whales and Beaked Whales.

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BIOGEOCHEMICAL DATA ASSIMILATION

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Introduction

Data assimilation is the systematic use of data to constrain a mathematical model. It is assumed that the dynamics that are responsible for a particular process or distribution are inherent in the data. By inputting data of various types into a mathematical model, the model, which is a truncated version of the real world, will more accurately stimulate a particular environment or situation. Through data assimilation, the hindcast, nowcast, and/or forecast of the model will be improved.

Data assimilation was first used in the 1960s in numerical weather forecasting models, with the goal of providing short-term predictions of meteorological conditions. The use of data assimilation techniques was made feasible by the development of a worldwide atmospheric data network that could provide the measurements needed. Data assimilation provided a methodology for using these observations to improve the forecasting skills of the operational models. Although weather forecasts are now taken for granted, to a large extent the accuracy of these forecasts results from assimilation of meteorological observations.

In the 1970s, numerical ocean general circulation models (OGCMs) became an important tool for understanding ocean circulation processes. Initial applications of these models focused on simulation of the large-scale structure of ocean currents. From these simulations, the limitations of the OGCMs were clear. Data assimilation was looked to as an approach for constraining these dynamical models with available data. For example, data assimilation could be used to quantitatively and systematically test and improve poorly known sub-grid-scale parametrizations and boundary conditions that are so abundant in OGCMs. With recent advances in data availability, it is also now feasible to use data-assimilative OGCMs for making forecasts of the ocean state, such as the El-Niño–La Niña cycle in the equatorial Pacific Ocean.

Implementing data-assimilative biogeochemical models has been problematic because of the paucity of adequate data. Historically, biological and chemical data were obtained almost exclusively by ship surveys, and thus were extremely limited in both space and time. However, advances in satellite and mooring instrumentation, as well as in the understanding of the structure and function of marine ecosystems, now makes it feasible to begin the development of data-assimilative biogeochemical