

## STUDYING HOW CETACEANS USE SOUND TO EXPLORE THEIR ENVIRONMENT

**Peter L. Tyack**

*Biology Department  
Woods Hole Oceanographic Institution  
Woods Hole, Massachusetts 02543-1049*

### ABSTRACT

Many biologists implicitly assume that mechanisms for echolocation and communication are separate and compartmentalized. For example, the high-frequency vocal and auditory specializations of dolphins are typically only discussed in terms of echolocation and the low-frequency sounds of baleen whales are usually presented as signals for long-range communication. However, signals that evolved for one purpose may develop other functions. Some porpoises appear to use rhythmic patterns of "echolocation" clicks as communicative signals. When a whale makes a low-frequency sound for communication, the sound may echo from the seafloor and possibly provide the whale with important information about its environment. Research on the evolution of echolocation in marine mammals suffers from a dearth of studies of ecological function and from a lack of broad comparative reviews. If studies of marine mammal sonar included more analysis of the problems for which sonar may have evolved, we might discover fascinating new kinds of biosonar. For example, low-frequency sound is better suited than high frequency for long-range sonar in the sea, and many targets of great importance to marine mammals, such as large bathymetric features and fish with resonant swim bladders are also well suited to low-frequency sonar. Some marine mammals have the skills required to engage in bistatic sonar, in which one animal may

listen to how the sounds of another individual are modified by the environment. Targets such as concentrations of fish with resonant swim bladders may absorb more energy than they scatter, leading to significant advantages for bistatic sonar in a forward propagation mode. These examples blend features typically associated with the domains of sonar and communication. I suggest that auditory and vocal skills evolved to function in one of these domains may preadapt animals for developing abilities in the other domain. Vocal learning, in particular, is required for many forms of sonar, and it also enables the evolution of very different communication systems than are possible when vocal output is unaffected by auditory input.

## INTRODUCTION

In spite of the considerable successes of research on cetacean biosonar, there are several unexploited opportunities. Extensive research has defined the biosonar signals produced by bottlenose dolphins, the performance of their echolocation, and specializations of their auditory system for echolocation. Yet we are ignorant of how cetaceans use echolocation in the natural environment. We know little about the targets for which this remarkable sensory ability evolved. In this paper, I will explore several new directions for research on how cetaceans may use sound to explore their environment. Our understanding of cetacean echolocation also remains isolated from research on acoustic communication, and I will discuss several potential interactions between auditory and vocal abilities evolved for echolocation and for communication.

The basic facts of dolphin echolocation are well known to most ethologists and are well summarized in Au (1993). Bottlenose dolphins produce clicks of very short duration (tens of microseconds, or less than 0.0001 sec), with energy well above the highest frequencies we can hear. Humans cannot hear well above 20 kHz, but dolphin echolocation clicks have energy above 100 kHz. Bottlenose dolphins can hear well at high frequencies, up to about 150 kHz. The auditory system of bottlenose dolphins is also specialized for rapid processing of very short signals. Bottlenose dolphins can detect small targets several centimeters in diameter out to ranges of about 100 m (Murchison 1980). Bottlenose dolphins can measure the distance to a target by timing how long it takes for an echo to return from one of their clicks, and they tend to wait to produce a click until they have processed the echo from the last click. Dolphins can discriminate targets of different composition, shape, or size.

Cetacean biosonar has been studied almost exclusively in captive bottlenose dolphins echolocating on artificial targets. Some of the first research on dolphin echolocation used fish as targets (e.g., Kellogg 1961). While these may be important targets for dolphins, their acoustic properties are complicated, and

were not quantified in these early studies. The use of artificial targets with simple and quantified acoustic properties represented an important advance in studies of dolphin echolocation. The early focus on bottlenose dolphins as subjects for echolocation research made sense as these were the most common animals in captivity and they are readily trained for experimental work. It was also a reasonable research strategy to concentrate on understanding one species in depth before including potential variation in echolocation across species.

In four decades of research on marine mammal echolocation, it is remarkable how few studies have used biologically relevant targets or species other than bottlenose dolphins. While we know a great deal about dolphin echolocation in a narrow artificial context, we know very little about how cetaceans actually use echolocation in the wild to solve problems of orientation, obstacle avoidance, and prey detection.

I believe that dolphin echolocation is at a point described by Griffin (1980) retrospectively for bats:

Something I should like to emphasize, because it may have implications for the future, is that after these basic facts [of bat echolocation] had been generally accepted there was what now seems in retrospect an incredible lack of interest in further studies of echolocation .... I cannot overemphasize the intellectual inertia and difficulty in justifying the necessary effort to continue studies of echolocation and inquire what further ramifications might develop after a wider variety of species had been studied under a wider range of natural conditions. We should be alert in the future for similar mental blocks that may restrict imagination and thus retard progress. (p. 4)

## EVOLUTIONARY COMPARISONS AND STUDIES OF ECOLOGICAL FUNCTION HAVE BEEN CENTRAL TO OUR UNDERSTANDING OF ECHOLOCATION IN BATS

Echolocation in bats has become a classic topic in ethology, sensory biology, and neurobiology, while echolocation by marine mammals is usually mentioned in passing, if at all, by most texts. This stems not merely from the difficulty of studying marine mammals, for both aerial bats and aquatic cetaceans live in environments that are foreign to humans. Both groups are extremely mobile in the wild and are difficult to maintain in captivity. The neurophysiological research which has uncovered many of the neural mechanisms underlying echolocation in bats has been facilitated by the greater availability of these animals than marine mammals for invasive research. However, new noninvasive methods are becoming available for neurobiological research. I believe that the more significant obstacle comes from less integration of psychophysical and physiological studies of cetacean echolocation with behavioral and ecological studies.

### Synergy between Studies of Behavioral Ecology and Sensory Physiology of Bat Biosonar

“From the beginning, the study of hearing in bats has been characterized by a synergistic partnership between behavioral and physiological approaches. The results have been nothing short of spectacular...” (Grinnell 1995, p. 1).

Studies of echolocation and communication benefit from synergy between naturalistic and experimental research. There are strong traditions of field studies of communication and experimental studies of echolocation in cetaceans, but there is little interchange between these approaches. Most studies of acoustic communication in cetaceans are observational studies, often in the wild, focusing on the acoustic structure and social functions of vocal signals as opposed to sensorimotor or cognitive mechanisms. Most studies of cetacean echolocation, as we have seen, involve experimental tests using captive dolphins and artificial targets. By contrast, many experiments in bat echolocation take as their starting point a detailed understanding of what signal the bat uses and what information it needs for a particular natural task.

For example, the earliest observations that stimulated interest in bat biosonar concerned the ability of bats to avoid large obstacles such as walls. Griffin (1974) initially studied obstacle avoidance in controlled experiments using evenly spaced wires. However, since many bats feed on insects flying at night, it seemed that bats might also use echolocation to detect their prey. Griffin and his colleagues therefore studied the sounds made by wild bats as they fed on flying insects. This research demonstrated that as bats pursued their prey, their biosonar signals became shorter with a more rapid repetition rate (Griffin 1974). Later work combined visual and audio recordings to define stages of predation as the big brown bat, *Eptesicus fuscus*, approached, tracked, and caught its prey, with each stage having characteristic frequency-modulated (FM) downsweep biosonar signals (e.g., Simmons & Kick 1983; Kick & Simmons 1984). The variation in biosonar signals with biosonar task helped to define how bats process these signals. The size, shape, and motion of prey targets coupled with the flight patterns of the bats also impose design constraints on bat biosonar that help narrow the range of appropriate biosonar mechanisms. The discovery of how echolocation is used to find prey fostered the development of experimental laboratory models of prey detection involving appropriate artificial or even synthetic models. These models have been critical for later research on biosonar signal processing by bats (e.g., Simmons et al. 1995).

Most flying insects that are preyed upon by bats flutter their wings at rates of roughly 10–100 times/second. This may seem to be a minor detail for bat echolocation, but this subtle feature of the bat’s environment is critical for the evolution of several important features of bat echolocation. Several species of bats from different families have independently evolved a biosonar signal that differs from the short FM downsweep of *Eptesicus*. These other species have a

long sound of a constant frequency (long CF) before ending the signal with an FM downsweep. These long CF/FM bats tend to feed on insects flying near wooded areas, where the surrounding objects are likely to return louder echoes than the prey of particular interest to the bat (Neuweiler 1990). The prey can be discriminated from this clutter, however, because their flying motion and fluttering wings change the frequency of the returning echo, just as a moving siren seems to change in frequency. This change in frequency due to the relative motion of source and receiver is called a Doppler shift. The long CF/FM bats have evolved a highly specialized biosonar system in order to resolve these small Doppler frequency shifts. Their auditory systems are specialized for detecting a narrow range of frequencies near the CF portion of their biosonar signal. This has been called an acoustic fovea, in analogy to the fovea of the eye, which is the area of most acute vision (Schuller & Pollak 1979). However, a feeding bat is moving as well as its prey, and its motion also causes a Doppler shift that could move the echo frequency outside of the foveal frequency band. These bats have evolved a precise compensation mechanism to shift the sound of their outgoing CF biosonar signals in order that the incoming echoes from prey will center on the optimal frequency for the auditory system. This compensation mechanism may lead to complex signal changes in the wild depending upon the relative velocities of bat and target. It was first demonstrated in an elegant lab experiment, using a stationary bat echolocating on a moving pendulum (Schnitzler 1968). The auditory systems of long CF/FM bats are incredibly sensitive to tiny shifts in frequency. For example the horseshoe bat, *Rhinolophus ferrumequinum*, can detect changes of < 50 Hz in an 83-kHz signal (Schuller et al. 1974) and the mustache bat, *Pteronotus parnellii*, can detect frequency modulations of as little as  $\pm 10$  Hz from a 60-kHz signal (Bodenhamer and Pollak 1983). The biosonar of these bats is sensitive enough to detect the wingbeat frequency of an insect. Von der Emde and Menne (1989) played synthetic wingbeat sounds to horseshoe bats, and found that these bats could detect changes as low as 2.8–4.6 Hz from a baseline wingbeat rate of 50 Hz. It has been suggested that they use this as a cue for discriminating insects with different wingbeat patterns (Schnitzler & Ostwald 1983).

### *We Need Closer Coupling between Field Observations and Experimental Studies of How Cetaceans Use Sound*

This feedback between studies of how bats use biosonar in nature and studies of sensory and neural specializations for bat echolocation has been central for the remarkable progress in this field. Insight into the particular problems for which bat biosonar has evolved has enabled experiments that give us a much greater appreciation for the sophistication of bat echolocation. There has been much less of this kind of feedback in research on cetacean echolocation. For example, there has been so little field observation of echolocation that more

than a decade after Norris and Møhl (1983) proposed that odontocetes can actually debilitate prey with their sonar signals, there still are no convincing data on the effects of clicks upon prey. While different biosonar signals produced by a bat species have been shown to be specialized for different biosonar problems, Au (1993) reports much less evidence that dolphin biosonar signals are similarly specialized for ecologically relevant problems. However, almost all of the experimental studies of dolphin echolocation involve stationary dolphins echolocating on stationary and artificial targets that bear little resemblance to the biologically relevant targets for which dolphin biosonar evolved. There is evidence in bottlenose dolphins (*Tursiops truncatus*), beluga whales (*Delphinapterus leucas*), and false killer whales (*Pseudorca crassidens*) of a correlation between the source level of an echolocation click and the peak frequency (Au et al. 1985, 1995, Brill et al. 1992). Dolphins have been shown to control the correlated source level or peak frequency of their clicks as a function of ambient noise (Au et al. 1985) or as a function of the echolocation task (Moore & Pawloski 1991), but these changes appear less specialized than those demonstrated for bat echolocation. Dolphin biosonar may in fact be much less specialized than bat biosonar. On the other hand, dolphin researchers may simply be unlikely to discover these specializations until they achieve a better integration of studies on the functions of biosonar in nature with psychophysical experiments of echolocation with captive animals and artificial tasks. For example, it will be particularly interesting to study whether there are any differences in how dolphins echolocate at different stages of searching, detecting, or pursuing prey, or when they or their targets are moving. Dolphins move and scan rapidly while echolocating. If they can process echoes equally rapidly, there may be tight coupling between a dolphin's search movements and its biosonar signal emission and processing.

#### *We Need a Broader Comparative Perspective of Cetacean Echolocation*

...echolocation sounds are consistent within a given species and differ in species-specific ways. Comparative studies show that these differences correlate with preferred habitats and hunting strategies. The differences also help establish the information-gathering value of different components of the echolocation sounds (Grinnell 1995, p. 2).

Studying the evolution of any specialized adaptation such as echolocation requires a broad comparative perspective (Harvey & Pagel 1991). Comparative studies also offer advantages to researchers interested in selecting an experimental subject for investigating biological mechanisms. Preliminary behavioral studies on diverse species may help direct experimenters to the best species for a particular problem. For example, when Griffin initially developed an interest in how bats echolocate to find prey, he went to a lake over which foraging bats

would fly straight and then dive with many rapid turns apparently in pursuit of an insect. Of the two bats common in the area, the little brown bat, *Myotis lucifugus*, produced FM downsweeps that varied in repetition rate, but that otherwise did not change much. However, Griffin (1974) did notice changes in the biosonar signals of big brown bats, *Eptesicus fuscus*. As the big brown bats flew to the lake, they produced a slow series of FM downsweeps. As a bat pursued its prey, the downsweeps became shorter with a more rapid repetition rate (Griffin 1974). These early field observations suggested that big brown bats would be better subjects than little brown bats for studies of how bats change their biosonar signals at different stages of predation. If bat researchers had limited their work to little brown bats, bat and dolphin sonar might seem similarly unspecialized. Au (1993) in his comprehensive review of dolphin biosonar suggests that "there is no solid evidence of dolphins purposefully changing the spectral content and duration of their biosonar signals when approaching prey or a stationary target." However, this conclusion stems almost exclusively from data on the bottlenose dolphin, which is a generalist in terms of foraging and habitat use. One might not expect a highly specialized sonar signal in such a species, and Ketten (1994) describes this species as having relatively unspecialized high-frequency hearing. There has been so little work on species other than the bottlenose dolphin that we do not know whether this is typical of other dolphin species. Aside from occasional references to beluga whales, *Delphinapterus leucas*, and the false killer whale, *Pseudorca crassidens*, the comprehensive review of dolphin biosonar by Au (1993) devotes only four pages to "signals from other species." This small percentage accurately reflects the limited work on other species, particularly by American biologists.

The lack of a broader array of comparative data makes it difficult to judge whether differences between species merely involve trivial details, or whether different species have evolved different biosonars designed to solve different problems. For example, Turl and Penner (1989) report that the interclick interval of bottlenose dolphins is greater than the two-way travel time from the click to the sonar target, while beluga whales will emit packets of clicks with shorter intervals. This suggests that bottlenose dolphins do not emit a click until they have processed the preceding echo, and that beluga whales, which sometimes emit a click before hearing the preceding echo, may have a different echolocation strategy. Among bats, there are clearly much more profound differences in the biosonar systems, for example, of the bats that analyze Doppler shifts in long CF signals versus those that use short downsweeps as biosonar signals. Specializations for long-duration constant-frequency signals, finely tuned hearing curves, and Doppler compensation have evolved independently in several distantly related groups of bats. The convergence suggests that this complex of traits forms an integrated biosonar system, perhaps evolved for hunting in environments where the echoes of insects are masked by background clutter (Neuweiler et al. 1988).

There are some hints of differences in the biosonar systems among the cetaceans that may parallel the differences in biosonar among bats. Several cetacean taxa, porpoises of the family Phocoenidae and dolphins of the genus *Cephalorhynchus*, have more specialized hearing mechanisms than those of bottlenose dolphins and biosonar signals that are longer in duration and narrower in bandwidth. These taxa have been identified by Ketten (1994) as having inner ears that are particularly specialized for high-frequency audition above 100 kHz. As an illustration of the different echolocation signals, Figure 1 compares clicks from a bottlenose dolphin and from a harbor porpoise. The echolocation signals of bottlenose dolphins in open water are very short in duration (40–70  $\mu$ sec), relatively broadband (80–154 kHz), and with high sound pressure levels (up to over 220 dB re 1  $\mu$ Pa at 1 m) (Au 1980). By contrast, the echolocation signals of phocoenid porpoises and *Cephalorhynchus* dolphins are 5–10 times longer (150–600  $\mu$ sec), roughly half the bandwidth (120–160 kHz), and with sound pressure levels between 150 and 170 dB, several orders of magnitude weaker than the loudest bottlenose dolphin clicks (*Phocoena phocoena*: Amundin 1991, Kamminga & Wiersma 1981; *Phocoenoides dalli*: Hatakayama & Soeda 1990;

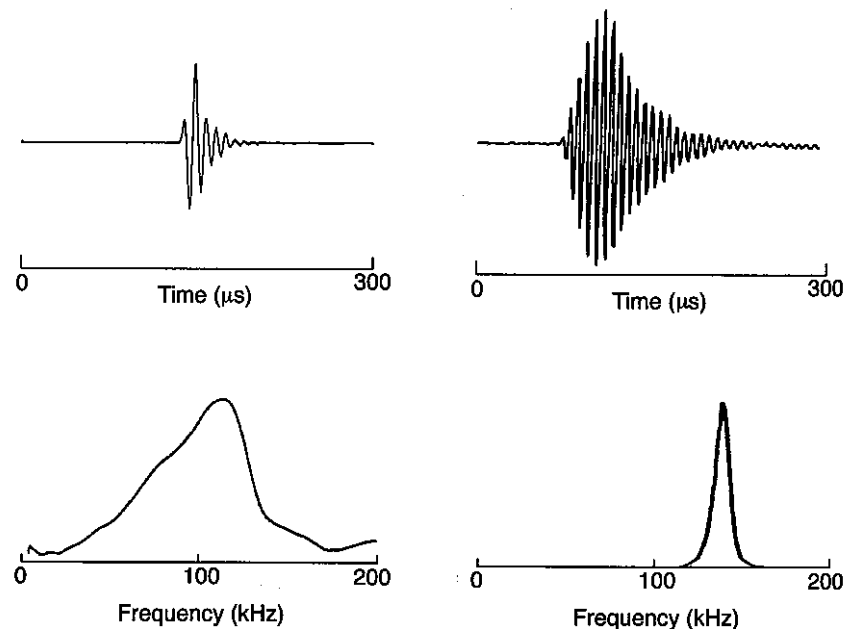


Fig. 1. Waveform (top) and spectra (bottom) of clicks from bottlenose dolphins, *Tursiops truncatus* (left) and harbor porpoise, *Phocoena phocoena* (right). Bottlenose dolphin figure is an average from an entire click train adapted from Au (1980). Harbor porpoise figure is from a single click from a young animal adapted from Kamminga (1988).

*Cephalorhynchus commersonii*: Kamminga & Wiersma 1982, Evans et al. 1988; *C. hectori*: Dawson & Thorpe 1990).

The analogy between porpoises and *Cephalorhynchus* with the long CF/FM bats can only be taken so far. The long CF/FM bats produce biosonar signals more than 80% of the time when they are echolocating (Fenton 1995). These bats can process information from an echo even while the bat is still producing the outgoing signal. This is presumably enabled by their Doppler shift compensation described above. On the other hand, dolphins, porpoises, and most other bats are actually producing outgoing clicks less than 20% of the time when they are echolocating. Most species tested adjust their outgoing pulses so as not to interfere with incoming echoes. The actual durations of porpoise and *Cephalorhynchus* echolocation signals are less than one tenth those of the long CF/FM bats, and most available information would suggest that they produce echolocation signals only for a low percentage of the time when they are echolocating. While porpoises and *Cephalorhynchus* appear to have inner ears tuned particularly for high frequencies and produce narrow band clicks, there have been no tests of whether they use Doppler information in their echolocation.

What I do want to suggest is that, as in the bats, the convergence of biosonar signals among distantly related animals suggests the evolution of a specialized biosonar system well worthy of further study. Watkins et al. (1977) and Dudok van Heel (1981) suggest that porpoises and *Cephalorhynchus* inhabit similar coastal habitats and have converged upon similar morphology and biosonar systems especially suited to this ecological niche. I am suggesting a convergence in echolocation systems of a sort that has been suggested by Endler (1992) for communication signals:

Thus, sensory systems, signals, signaling behavior, and habitat choice are evolutionarily coupled. These suites of traits should coevolve in predictable directions. (Endler 1992, p. S125)

More research on a variety of cetacean species is needed to enable the kinds of comparisons that have proven so productive in studies of echolocation and communication in other taxa.

#### ACOUSTIC CHARACTERISTICS OF BIOLOGICALLY RELEVANT TARGETS FOR MARINE MAMMAL BIOSONAR

Our ignorance of how wild marine mammals use sound to explore their ocean environment contrasts markedly with the enormous effort of underwater acousticians in exploring how humans can use sound to find out about the ocean. Humans map the bathymetry of the sea using ever more sophisticated sonars. Where pelagic fishing once depended upon large doses of luck, fish-finding

sonars have become so good as to take the luck out of this kind of fishing. Any predator-prey ecologist would immediately appreciate the sophistication of military sonars used for antisubmarine warfare, along with the counter measures employed against these sonars. The field of acoustic oceanography in the last few decades has developed the analytical tools and data to start to understand the opportunities and problems which ocean acoustics offered for marine mammals during their tens of million years of adaptation to life at sea. Acoustic oceanography allows biologists to develop models of how sound might be used to solve specific problems encountered by marine mammals. These models will usually specify design features for sounds used to solve the problem, as well as set bounds on what sounds, receivers, and signal processing are feasible or optimal. For example, a sonar designed for depth sounding is likely to have very different signals, receivers, and processors from a sonar designed to classify different species of plankton.

In order to broaden the scope of our thinking about how marine mammals use sound to explore their environment, I will therefore explore the acoustic properties of some biologically relevant targets. Underlying this examination is the assumption that the acoustic properties of targets are important sources of selection for animal biosonar systems. In analogy to bat research, are there marine equivalents to fluttering insects, targets whose acoustic properties may hold the key to how animals use sound to explore their environment? The implications of this discussion for animal biosonar will necessarily be speculative, but my goal is to direct research attention to potentially important problems that are not being studied. I will therefore particularly focus this discussion on animals and biosonar problems that have not been studied in captivity.

The high-frequency specializations of bats and dolphins form the basis for our understanding of echolocation. High-frequency sounds are particularly useful for detecting echoes from small targets or for increasing the resolving power of a sonar used with objects that are larger than the wavelength of the sonar signal. However, high frequencies of sound do not in general propagate as far as lower frequencies (Urlick 1983). Fenton (1995) agrees with Griffin (1974) that bat echolocation typically operates at short ranges up to several tens of meters. The high-frequency echolocation system of coastal bottlenose dolphins has detection ranges of about 100 m (Murchison 1980). Cetaceans inhabit a broad range of habitats. Some may dive more than a kilometer below the surface, and pelagic species may migrate thousands of kilometers. Many of these species face problems where they would benefit from sensing features of their environment at ranges well beyond the demonstrated detection range for dolphin clicks. A variety of sensory modalities are available to animals to solve these problems. Deep-diving seals may rely upon vision that is sensitive to low light levels at depth (Schusterman 1972), while migrating animals may rely upon a remarkable variety of cues for orientation, including visual, acoustic, olfactory, and magnetic (Schmidt-Koenig 1975; Papi 1992). However, seafaring humans have quickly

recognized the utility of acoustics as a distance sense in the sea where vision is usually limited to tens of meters. Many marine sonars developed by humans use frequencies well below those of bats or dolphins in order to operate at these greater ranges. Since we know that many cetacean species specialize in low-frequency acoustics for communication, it seems reasonable to explore whether they might also use lower-frequency sounds to explore their environment at greater ranges.

Many important marine targets will reflect low-frequency sounds of the sort usually thought to be used by cetaceans for social communication. Marine mammals with unspecialized hearing may be able to obtain important information about their environment by simply learning how to interpret echoes from these signals. Some reviews of the negative evidence concerning high-frequency echolocation in whales and seals clearly consider this possibility (e.g., baleen whales: Herman 1980, Moore 1980; pinnipeds: Schusterman 1981). In order to distinguish between highly specialized abilities for echolocation of the sort demonstrated for bats and dolphins, and the more general abilities to use audition to learn about the environment, I will follow the usage of Kinne (1975) and use the term *biosonar* to include these more general abilities. This matches the broad range of applications called *sonar* in engineering as well. In a later section of this paper, I will consider the possibility that animals may use several forms of sonar which are familiar to sonar engineers, but are very different from what biologists think of as echolocation. I would like to emphasize that when I discuss animal biosonar in this sense, the term does not presume a specialization of sensory ability. Rather I want to focus on the potential utility of sound as a distance sense for marine mammals to learn about their environment. If marine mammals can use general mammalian auditory abilities and nonspecialized vocal signals to obtain information about their environment, this may illuminate potential pathways for the evolution of more specialized adaptations for high-frequency echolocation.

## Sensing the Physical Environment in Bottom and Surface Reverberation

### *Bottom Reverberation*

Humans have devoted billions of dollars to developing techniques to use sound to explore the seafloor and sediments below it. This effort provides extensive theory and data on the design features of echosounding. Different frequencies of sound have different properties of reflecting off the seafloor or penetrating it and reflecting off inhomogeneities in the sediments below. The frequency range of sounds that penetrate sediments well is typically below 100 Hz. The amount of sound energy reflecting off a rigid object drops rapidly if the circumference of the object is less than the wavelength of the sound. The speed

of sound in seawater, denoted by the variable  $c$ , is about 1500 m/sec. The relationship between wavelength,  $\lambda$ , speed,  $c$ , and frequency,  $f$ , is:  $\lambda = c/f$ . This means that the wavelength in seawater of a 15-Hz whale call would be 100 m; that of a 150-Hz call, 10 m. These long wavelengths would not be useful for detecting small objects, but do reflect off of large bathymetric features. Wavelengths smaller than the circumference of the target are still effective, so higher frequencies can also be used for detecting large targets. For example, the seafloor is a very large target, but depth sounding sonars often use frequencies of 3.5 or 12 kHz, with wavelengths of 43 cm and 12.5 cm. Echo sounders typically have a downward-directed pulse and measure the time until the first reflection. With a nominal sound speed of 1500 m/sec, if there were a 4-sec delay between the pulse output and the echo, then the seafloor would be 3 km below the ship.

### Depth Sounding

The simplest of echo sounders simply detect a single echo in order to estimate range from the bottom. Some animal sounds have long been known to have the potential for this kind of depth sounding. Griffin (1955) analyzed what appeared to be calls and bottom echoes from an unknown marine animal dubbed the "echo fish." The "echo fish" recordings were made using a surface hydrophone in waters 5100 m deep. "Echo fish" calls were 500 Hz in frequency and 0.3–1.5 sec in duration. Each of these calls was followed by an apparent echo 1.47–1.77 sec later, with an echo intensity only 27%–56% the amplitude of the initial call. Since the speed of sound in the ocean is about 1500 m/sec, the difference in path length between the direct and apparent bottom reflected path was about 2400 m. The strength of both signal and echo led Griffin to speculate that the source was probably not at a great distance from the hydrophone. In the simplest case, if the "echo fish" were directly below the hydrophone, then it would have been 1200 m above the seafloor or 3900 m deep. This "echo fish" was likely also to have heard these echoes, and might also have been able to time the echo delay to estimate its distance from the seafloor.

An echo sounder would clearly also be useful to a marine mammal that dives rapidly and deeply. Sperm whales, for example, routinely dive from 300 to over 1000 m in dives that last around 40–50 minutes. Sperm whales tracked with a sonar descended at rates of 1–2 m/sec (Papastavrou et al. 1989). The rate of descent of sperm whales tagged with a transponder tag averaged about 1 m/sec with a maximum of 4 m/sec (Watkins et al. 1993). These tagged whales were within a few kilometers of the island of Dominica. If one of these whales had no way of detecting the bottom, it clearly would have run a risk of collision. However, when sperm whales start a dive, they are reported to start regular series of clicks as they reach depths of 150–300 m (Papastavrou et al. 1989). These clicks are similar enough to those from some depth sounders that Backus and Schevill (1966) report that sperm whale clicks actually can make false targets

on a ship's depth sounder. Male sperm whales produce particularly loud clicks with a slow repetition rate (Weilgart & Whitehead 1988). In waters off Dominica, bottom reverberation has been recorded from these slow clicks. Figure 2 shows a spectrogram of one such click followed by reverberation as such a nondirectional click echoes off the surrounding bathymetry. These echoes were received 1.4 seconds after the direct click, indicating that the echo path was over 2100 m longer than the direct one. While the echoes from the slow click shown in the figure are more obvious at these ranges than those from the regular clicks that can be seen in the center of the figure, clearly a whale producing regular clicks would be likely to hear echoes from the seafloor as it approached within a few hundred meters of it. Whatever other reasons a whale might have for producing the clicks Weilgart and Whitehead, (1988) a diving whale would do well to heed such echoes as a warning of an approaching obstacle.

When you listen to the pattern of bottom reverberation shown in Figure 2, you can hear a pattern of several returns, presumably as the omnidirectional

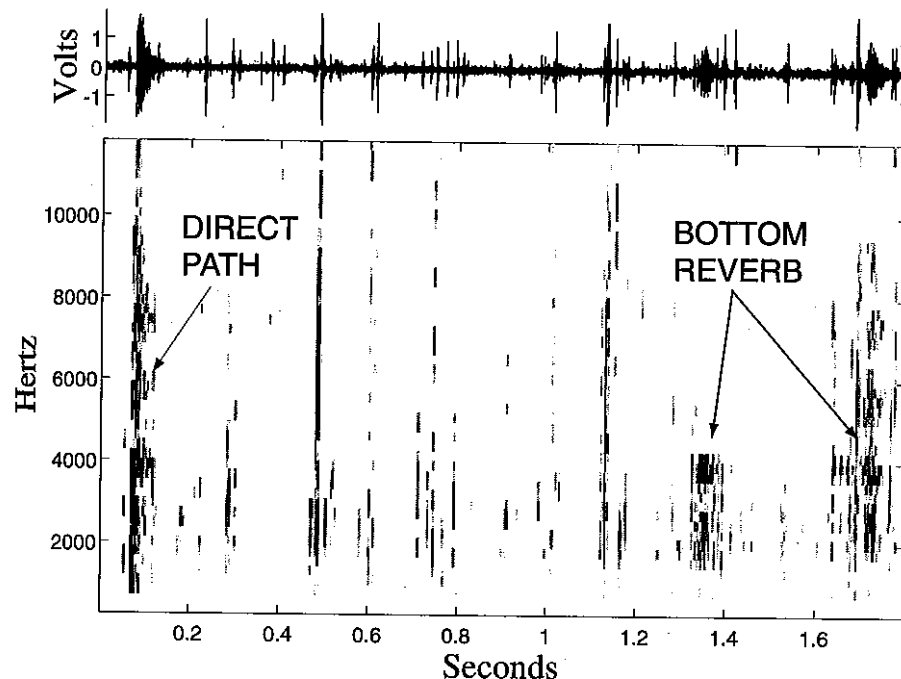


Fig. 2. Spectrogram of slow click from a sperm whale, *Physeter macrocephalus*, in waters near the island of Dominica in the Caribbean. The direct arrival of the click is visible on the left of the spectrogram, and echoes of the click reflecting off the seafloor are visible on the right of the spectrogram just before 1.4 and just after 1.6 seconds. The shorter clicks in the middle of the spectrogram are regular clicks from sperm whales.

sperm whale click reflects off a variety of bathymetric features in the vicinity. We do not know how well sperm whales can locate sounds such as echoes, but the ability of dolphins to locate sound sources has been tested. Bottlenose dolphins can differentiate signals separated by several degrees (Renaud & Popper 1975). If sperm whales have comparable abilities, then they might be able to separate the superposition of echo returns from different bearings and ranges shown in Figure 2 into some sort of bathymetric map or image. Pack and Herman (1995) have shown that bottlenose dolphins can use either echolocation or vision to form an internal "image" or percept of complex shapes, with spatial information that is readily integrated across these senses. If a whale were able to update bathymetric maps from successive clicks, this might be integrated with vestibular input for acoustic orientation.

#### Use of Bottom Reverberation for Navigation

The last paragraph suggests that marine animals may be able to do more than just perceive the depth of the seafloor, but may also be able to perceive the bearings of echoes from targets that are not directly below. Figure 3 shows a

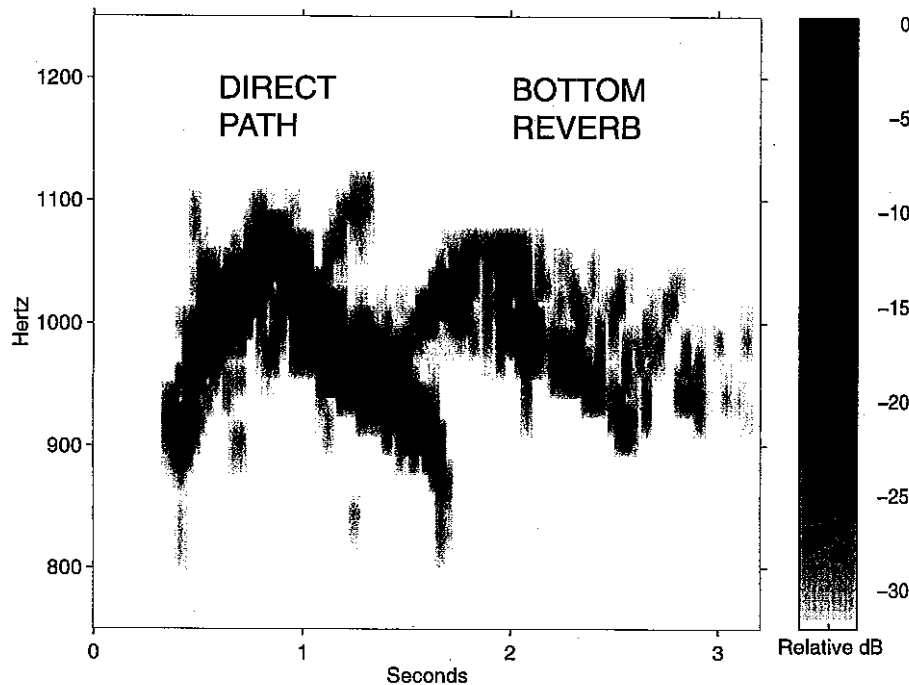


Fig. 3. Spectrogram of a unit from the song of a humpback whale, *Megaptera novaeangliae*, from 0.5 to 1.8 seconds and a bottom echo of the same sound from 1.6 to 3 seconds.

simple dominant echo from one sound of a humpback song. The whale recorded here was swimming in deep water a few kilometers offshore of an oceanic island. If the whale whose song is shown in Figure 3 could localize the bearing of the echo in the setting recorded here, these echoes would be likely to indicate the direction of rapidly shoaling water. Many recordings of humpback song in similar settings show such bottom reverberation. Tyack (1981) argues that humpback song appears to be a reproductive advertisement display with a primarily communicative function. During the breeding season, many humpbacks congregate on shallow banks where females have young and where there is a high density of singers. However, humpbacks sing far from the known concentrations of breeding females, and they sing during some phases of their annual migrations (Clapham & Mattila 1990). In these settings, bottom reverberation may provide them with useful information about their environment.

Several biologists have suggested that marine mammals might be able to sense echoes of low-frequency vocalizations from distant bathymetric features in order to orient or navigate (Norris 1967, 1969; Payne & Webb 1971; and Thompson et al. 1979). For example, if the 20-Hz signals of finback whales were designed to avoid overlap between outgoing pulse and returning echo, then the 1 sec duration of these signals coupled with the 10–30-sec interpulse interval would suggest an effective range of from 1 km to several tens of km. It has been suggested that these characteristics are not well suited for echo sounding in these whales, which are not thought to dive deeper than several hundreds of meters (McDonald et al. 1995). Payne and Webb (1971) evaluated the hypothesis that finbacks might use these pulses for a bathymetric sonar with ranges of tens of km. They concluded that signals with these frequencies and source levels could function for a long-range bathymetric sonar but they questioned the appropriateness of the very regular and relatively short repetition rate of the pulses for use as this kind of biosonar. In particular they question why animals slowly meandering in a restricted area would require such frequent updates of bathymetry. Payne and Webb (1971) and Watkins et al. (1987) both suggest that these signals appear primarily to have evolved for long-distance communication. These analyses all assume that whales must wait for the echo to return before they emit the next signal. However, blue whale calls are quite long, with both CF and FM segments, somewhat similar to the long CF/FM calls of bats. CF/FM bats can process an echo even while the signal is still being emitted. Beluga whales also are capable of emitting "packets" of clicks with interpulse intervals less than the round-trip travel time to the sonar target (Turl & Penner 1989). Whales may not have to process each pulse independently, waiting for the echo return before emitting the next pulse, but rather they may be able to process whole series of pulses in ways that improve their sonar performance. Clark (1993) has suggested that the low-frequency calls of finback or blue whales would produce easily identifiable echoes from seamounts hundreds of kilometers away, and he speculates that this would provide important cues for navigation during migration or



transits across the deep ocean. Even if these signals have a primarily communicative function, these whales may also detect and respond to reverberation from bathymetric features.

#### *Testing Sensory Mechanisms for Orientation in Cetaceans*

My primary reason for bringing up the potential use of sounds for orientation or echo sounding is to direct our focus on the sensory mechanisms which marine mammals use to solve problems posed by their natural environment. By focusing on a particular problem of biological significance, we can explore the range of sensory mechanisms that an animal might use. Kinne (1975) emphasizes that animals of many species integrate information from a variety of senses in order to orient in space. Several different mechanisms have been suggested for long-range orientation by cetaceans, including detection of geomagnetic cues (Klinowska 1985; Walker et al. 1992; but also see Hui 1994), visual monitoring of celestial cues (e.g., Busnel & Dziedzic 1966), and landmarks (Pike 1962). The temperature, salinity, and movement of the surrounding water may also provide important cues for marine mammals (Norris 1974). Regarding sensory mechanisms for estimating depth, Kinne (1975) suggests that marine mammals may be able to detect increasing pressure with increasing depth. None of these mechanisms have been tested directly in orientation experiments.

Since marine mammals are very sensitive to a variety of sensory cues, it is unlikely that observational data alone will suffice to demonstrate which senses are necessary and sufficient for tasks such as orienting with respect to the seafloor. Experimentation with captive dolphins under controlled conditions has been critical for elucidating echolocation, but large whales are difficult to maintain in captivity. How might one experimentally test whether whales use echoes from their sounds in order to orient with respect to the seafloor? One opportunity is opened by a device called an echo repeater. These are used for testing man-made low-frequency sonar systems. The echo repeater constantly monitors sound with a hydrophone. When a potential sonar signal is detected, the repeater electronics modify the signal as if it had reflected from a specific kind of sonar target. An outgoing pulse is then generated using a sound projector in order to simulate a real echo from the target. Large targets such as the seafloor would be difficult to emulate, because a signal from one projector would not have the spatial complexity of reverberation from the large target. We would need more observation of tagged whales swimming near bathymetric features and potential obstacles in order to predict a response to a synthetic echo from an echo repeater. However, if, for example, sperm whales use echoes from their clicks in order to avoid collision with obstacles, then presumably they would slow in response to a synthetic echo indicating they were closing on an obstacle. If one could place such a repeater in the path of a whale whose movements were being monitored, one could evaluate how the whale responds to a synthetic echo

indicating an apparent obstacle. One could use precisely the same outgoing signal as a control stimulus if its playback were not contingent with the whale having just produced its own sound. Most biosonar estimate range to a target by measuring the time delay between a vocalization and when the echo returns. If whales attend preferentially to echoes from their own sounds, they would be likely to respond more to the contingent echo playback. On the other hand, if whales simply habituate to such reverberation as noise, and if they respond to novel and unexpected stimuli, then they might be expected to show a stronger response to the noncontingent "echo."

Comparisons between different species may help elucidate different mechanisms for problems such as detecting the seafloor. Elephant seals, for example, have a dive pattern that can compete with sperm whales. When at sea, they spend 90% of their time underwater, and dive to depths of 1500 m or more. The average rate of descent of adult female elephant seals averages around 2 m/sec (Le Boeuf et al. 1988). Elephant seals are not known to vocalize underwater and have large eyes that appear to be specialized for vision at low light levels. We know little about the variety of sensory cues used by deep-diving mammals to orient at depth. While there is little downwelling light at the depths to which these animals can dive, especially at night, they might be able to use bioluminescence in order to detect prey or the seafloor. In order to resolve these questions, we must obtain detailed dive data along with the relevant sensory stimuli. Both elephant seals (Le Boeuf & Laws 1994; Fletcher et al. 1996) and sperm whales (Watkins et al. 1993) can be tagged with large enough packages to record or telemeter data such as depth of dive, acoustic data, and light levels. Deployment of such tags on these animals will help identify likely cues and detailed responses that will facilitate the development of experimental manipulation of sensory cues.

While discussions of long-range orientation among cetaceans typically focus on migrating baleen whales, most toothed whales are also highly mobile, ranging on the order of 100 kilometers/day, well in excess of terrestrial carnivores and primates (Wrangham et al. 1993). For example, killer whales are reported to swim at an average speed of 5 km/hr, and to have day ranges of 80–160 km/day (Kruse 1991). A young male pilot whale tracked in the North Atlantic covered 7588 km in a 95-day interval. He moved an average of 80 km/day with a maximum daily movement of 243 km (Mate 1989). Our developing ability to track the movements of these animals may be coupled with experimental manipulation of sensory cues in order to conduct field experiments on the sensory bases of orientation in marine mammals.

#### *Reverberation from the Sea Surface*

While most people are more familiar with the idea of sound reflecting off the seafloor, the interface between sea and air also reflects sound energy. Sound energy

that reaches a sensor after scattering from the sea surface is called sea surface reverberation, and it can exert a significant influence on acoustic signals in the sea. Reverberation from the sea surface and the seafloor can greatly modify the original signal. However, these modifications do not necessarily just reflect degradation of the signal. The ways in which reverberation modifies the original signal can inform an animal about its environment. For example, diving mammals have a variety of ways to plan their dives, but it may often be useful for them to be able to determine how deep they are in order to estimate the time for ascent. Echoes from the sea surface could inform a diving animal of range to the surface.

Many marine mammals live in polar waters where the sea surface is covered with ice. For example, bowhead whales, *Balaena mysticetus*, migrate in the spring across the ice-covered Beaufort Sea, finding leads in the ice far offshore (Braham et al. 1980). Beluga whales have also been sighted many hundreds of kilometers north of the Beaufort Sea coast deep in Arctic pack ice. Finding breathing holes is a life-or-death problem for animals that dive under the ice. Downwelling light is likely to be an important stimulus during periods of daylight, but there are extended periods with low light in polar regions. Martin (1995) tracked beluga whales frequently diving to depths greater than 500 m under heavy ice. He suggests that they use these deep dives to scan for distant breathing holes, using either vision or acoustic cues. Seals have been shown to rely upon vibrissal sensation to find holes in ice when vision is limited, but this only functions at relatively short ranges (Watkins & Wartzok 1985). Ice makes such a good acoustic target that some of the first human sonar systems were developed to detect icebergs after the Titanic disaster (Clay & Medwin 1977; Hunt 1954). The problem of how cetaceans detect large ice obstacles or breathing holes in ice has been little studied. Clark (1989) and George et al. (1989) described how vocalizing bowhead whales, *Balaena mysticetus*, avoided a large floe of multiyear ice at ranges much farther than the limit of underwater visibility. Ellison et al. (1987) speculated that bowhead whales might be detecting the ice floe by listening for echoes from their own vocalizations.

There is a significant physical difference in how underwater sound reflects off an air interface compared to a denser surface. When sound in the dense aqueous medium reflects off of the air surface, there is a reversal in phase of the reflected wave (Horton 1959). This phase reversal is clearly visible when we analyze the details of the waveform of a signal. For example, Figure 4 shows on

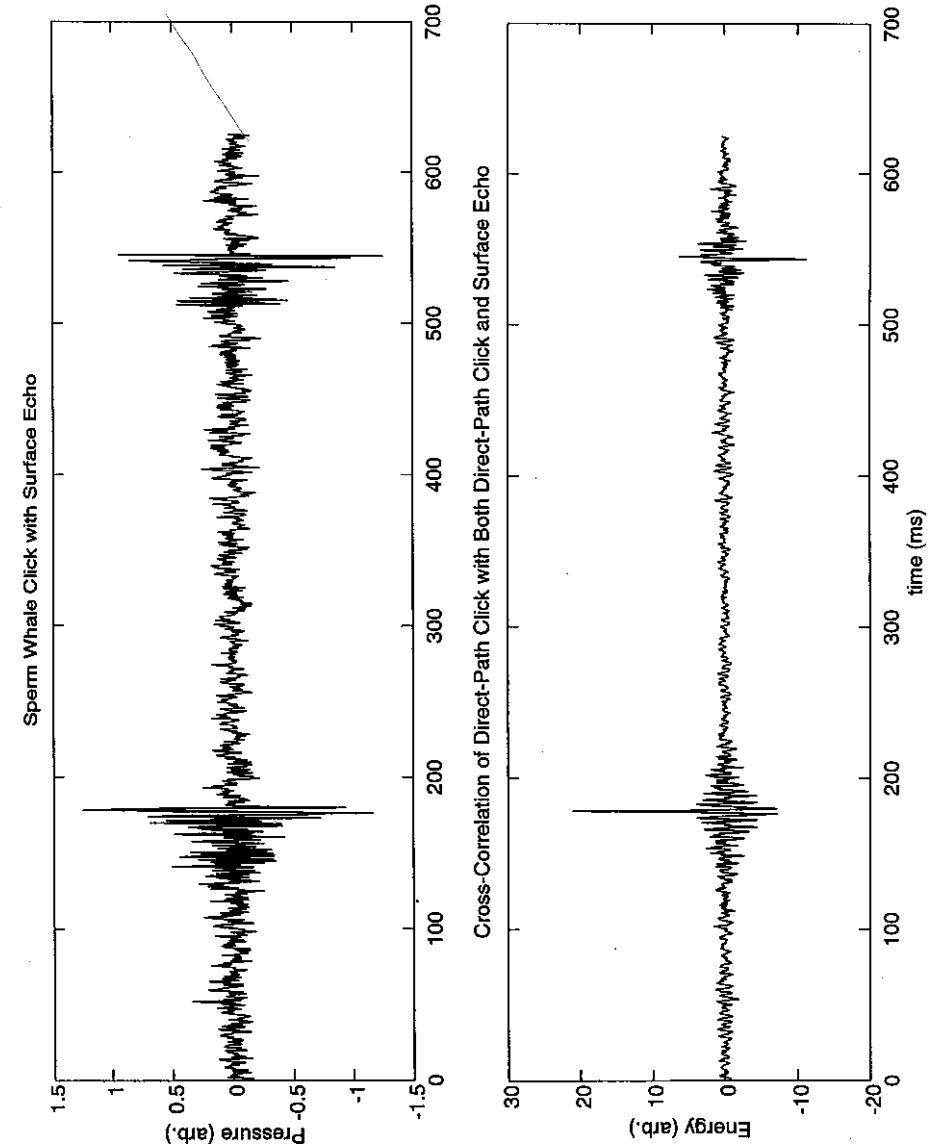


Fig. 4. Left: waveform of the direct path of the click of a sperm whale at 150 to 200 msec and an apparent surface echo of the same click at 500 to 550 msec. Right: Cross-correlation of the direct-path click (from 150 to 200 msec) against the full waveform. The positive peak at 180 msec is the autocorrelation of the click against itself. The negative peak at 550 msec indicates that the surface echo has a phase that is reversed compared to the direct-path click (see text).

top the waveform of a sperm whale click. On the left is the direct path of the click, and on the right is what appears to be a later arrival of an echo from the sea surface. The phase reversal can be seen on the bottom of the figure, which shows the cross-correlation of the direct path version of the click with the rest of the waveform. The click shows a strong positive peak at 180 msec as it correlates with itself, and a strong negative peak where it correlates with the surface bounce at 550 msec. This negative peak indicates that positive pressures in the direct path correlate with negative pressures in the surface echo and vice versa. This is indicative of the phase reversal of a surface reflection. Many models of marine mammal hearing and echolocation treat the auditory system as one which simply integrates energy over a time interval (Au 1993). This differs from much work with bats, which suggests that some bats are sensitive to the differences between the phase of an outgoing signal and incoming echo (e.g., Menne et al. 1989). The peripheral auditory system of most mammals is capable of following waveforms at least at low frequencies. Given the potential biological relevance of the phase reversal from the sea surface, experiments on whether marine mammals can detect phase reversals may help us to determine whether marine mammals may have similar abilities.

#### *Sensing Biological Targets in Volume Reverberation*

When sound is scattered by objects or inhomogeneities within the water column, underwater acousticians call this volume reverberation. There are a large variety of potentially significant targets for marine mammals within the water column, including conspecifics, predators, and prey. Much of what we know about dolphin echolocation involves using high-frequency sound to detect echoes that reflect from solid objects in the water column. This mode of biosonar operation would function well to detect fish or similar small targets at ranges of up to 100 m or so. However, many of the fish or zooplankton prey of marine mammals are schooling species and occur in a highly patchy distribution both in time and space. Marine mammals that feed on them often face serious problems for finding aggregations of prey within large areas of ocean. Very little is known about how cetaceans find patches of prey on the order of 10 m in size at ranges on the order of kilometers. Physical inhomogeneities due to differences in the temperature or salinity of water may also scatter sound. These boundaries between different water masses often are correlated with high concentrations of planktonic prey (Parsons et al. 1984). If whales were able to detect these boundaries at large ranges, they might be able to use this to find high concentrations of prey.

A major difference in echolocation of marine vs aerial animals concerns the density of the medium versus the density of biologically relevant targets. Seawater is much denser than air. Many biologically significant targets are animals or plants, and these are often roughly the density of water. Biosonar

targets of aerial echolocators tend to be much denser than the air medium, and they are efficient reflectors of airborne sound. However, since animate targets are roughly the same density as seawater, these excellent targets in air will reflect less sound energy when in an aqueous medium. One of the most important targets in the sea consists of air bubbles or gas-filled cavities (Clay & Medwin 1977). These are the biological targets that provide a difference in acoustic impedance as great as the fluid-filled targets that are so important in airborne biosonar. Bubbles also resonate at surprisingly low frequencies. Sound energy drives a bubble into a resonant oscillation at a wavelength much longer than that of the physical circumference of the bubble. For example, the resonant frequency,  $f$ , of a bubble with a 1 cm radius near the sea surface is 326 Hz (Urlick 1983, p. 251). Yet the wavelength,  $\lambda$ , of this frequency in seawater with a sound speed  $c = 1500$  m/sec is  $\lambda = c/f = 1500/326 = 4.6$  m or 460 cm. An air-filled spherical bubble also has a very narrow frequency range for its maximum resonance (Stanton 1989).

#### *Fish Swim Bladders and the Air-Filled Lungs of Mammals as Biosonar Targets*

Bubbles are particularly relevant targets for our discussion because there are several targets of biological interest that are air-filled. The lungs of marine mammals are inflated during at least part of their dive, and this can produce a strong biosonar target (Love 1973). Many fish species that are prey for cetaceans have gas-filled swim bladders that are used for buoyancy regulation, as well as sound production and reception. Most swim bladder fish would have negative buoyancy if there were no gas in the bladder. These swim bladders are not spherical and they are constrained by the body of the fish, but their acoustic properties are roughly comparable to bubbles. The resonant frequencies of these swim bladders are surprisingly low in frequency given the size of the fish. For example, Batzler and Pickwell (1970) reported that a small anchovy at one atmosphere of pressure had a resonant frequency of 1275 Hz.

Many cetaceans feed on fish with swim bladders. Delphinids produce high-frequency echolocation clicks while feeding, but are also reported to produce a variety of pulsed sounds with energy below 5–10 kHz. These have typically been considered as communicative signals (e.g., Caldwell & Caldwell 1967), but Marten et al. (1988) suggest that they are also associated with feeding in bottlenose dolphins and killer whales. Many large whales also feed on small schooling fish such as anchovy, and many of these whales produce low-frequency sounds during the feeding season, but little is known about the function of these sounds. I believe that it would be well worth more detailed effort to compare the spectra of sounds produced by cetaceans against the target spectra of their prey. If the low-frequency resonance of fish with swim bladders were significant target characteristics, one would predict especially clear differences for species that feed on several different prey, some with gas-filled cavities and

some with none. For example, individual humpback whales may feed on schooling fish at some times and on schooling crustaceans at others. If they use their sounds to detect swim bladders, then one would predict more vocalizations or more emphasis on frequencies near the resonance of the swim bladders when they feed on fish.

The deep scattering layer is one of the dominant targets for reverberation within the water column. This is a layer of organisms living in the open ocean, which shows a vertical migration on a diurnal cycle. Hersey and Backus (1962) review data on the frequency dependence of echoes from the deep scattering layer. They found that deep scattering layers tend to have a strong frequency peak in the range from 2.5 to 25 kHz. Many cetaceans feed on deep scattering layer organisms, particularly at night when the layer rises toward the surface. If they are feeding on organisms which reflect acoustic energy in the 2.5–25 kHz range, they might also benefit from echolocation signals containing energy in these lower frequencies in order to receive echoes backscattered from these targets. The optimal signal would depend not only upon the resonant characteristics of the target, which change with depth, but also upon absorption (which favors lower frequencies) and ambient noise (which usually favors higher frequencies). Echolocation signals designed for longer-range detection of aggregations of deep prey may be particularly useful as animals are making decisions about when and where to start a feeding dive.

When biologists think of animal biosonar, they usually think of an animal making a sound and then listening for echoes reflecting off of targets nearby. Many fish-finding sonars operate in a similar fashion, as have most of the sonars which biologists use to study organisms in the ocean. Sonar engineers call this a monostatic sonar, in which both the sound source and receiver are in the same place (top row Figure 5). In the biological case, this means that the animal receiving the echo also produced the original signal. Some man-made sonars are designed for a bistatic mode, in which the sound source is received by a distant receiver (e.g., Curran et al. 1994). Bistatic sonars can either detect sound backscattered from a target (middle row Figure 5), or if they are oriented in line with the source and target, on the opposite side of the target than the source (bottom row Figure 5), then they can detect attenuation of the source signal induced by passage through the target.

The acoustic properties of a target may differ depending upon whether it is measured by backscatter (the scattering target strength) or by forward propagation. The target strength measured by forward propagation can be called the extinction target strength, because what is measured is the reduction in sound energy after passage through the target. Clay and Medwin (1977) compare the amount of incident sound energy scattered from an air bubble to the total amount of sound extinction. The extinction target strength is greater than that measured by scattering in this theoretical analysis. This suggests a further advantage for

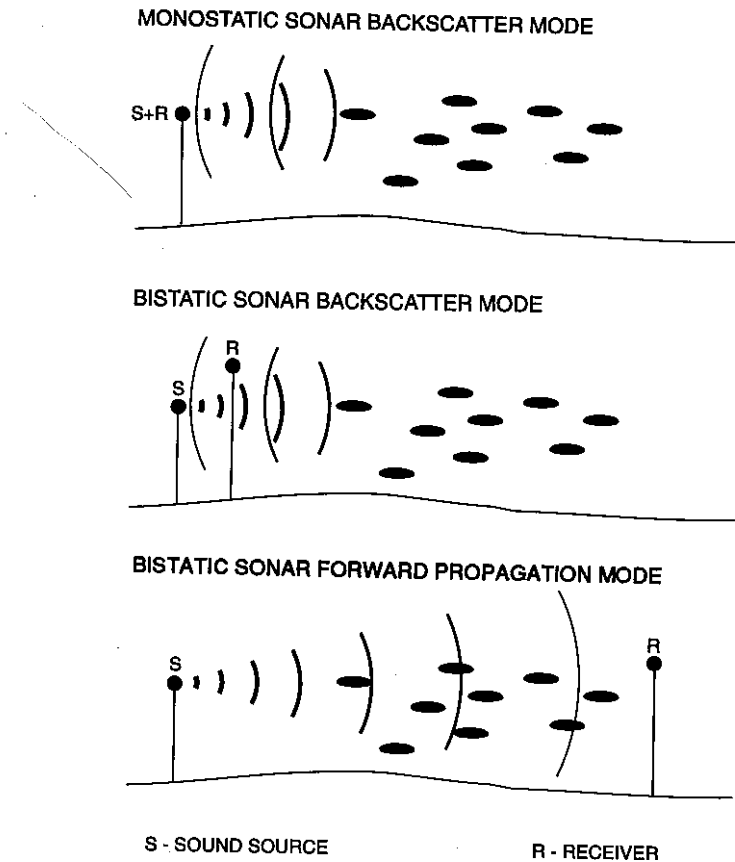


Fig. 5. Illustrations of three basic kinds of active sonar. Top: a monostatic sonar in the backscatter mode. The term monostatic implies that the source and receiver of the sonar are very close together (in biological terms, they are part of the same individual). A sonar operating in backscatter mode detects the echoes reflected back from a target. Middle: a bistatic sonar in the backscatter mode. A bistatic sonar has a receiver separated from the source (in biological terms, the receiver would be a different individual than the source). Bottom: a bistatic sonar in the forward propagation mode. A sonar operating in forward propagation mode does not detect echoes reflected from the target but rather detects modifications to the original signal that are caused by passage through the target.

forward propagation sonar to detect resonant gas-filled targets such as fish with swim bladders.

The limited data on detecting fish with forward propagation sonar suggest that fish with swim bladders may in some settings absorb significant sound energy in specific frequency ranges. Weston (1967) studied attenuation in signals received 137 km away from a 1-kHz source in the Bristol Channel. Just after sunset, he reports a drop of 30 dB in level of this 1-kHz noise. He associates this

with the fish along the axis of the beam dispersing from daytime schools into a diffuse dispersion that would cause more attenuation. Diachok (1996) and Diachok and Ferla (1996) measured sound absorption at a range of 12 km in shallow water in the Mediterranean Sea. They also report absorption losses of up to 25 dB at sunrise from pelagic schooling fish. Hersey and Backus (1962) reported that the resonant frequency recorded from a deep scattering layer shifted upward in frequency as the layer migrated downward. As these fish swam deeper, the increasing pressure would compress the gas in their bladders, causing it to decrease in volume and buoyancy. Fish can use active gas transport mechanisms in order to maintain an appropriate bladder volume for neutral buoyancy as they change depth. Diachok and Ferla (1996) also associated this frequency shift with vertical migration of fish. These data were obtained in the Mediterranean in areas of high density of sardines and anchovies, and the resonant frequencies they observed were consistent with those expected from sardines. The data presented by Diachok (1996), Diachok and Ferla (1996), and Weston (1967) suggest that there would be quite easily detectable dropouts or attenuation of sound around 1 kHz for a source and receiver separated by ranges of one to tens of kilometers when the path intersected with high concentrations of fish.

This discussion of biosonar targets absorbing sound energy may sound unusual to biologists. A bistatic biological sonar would be one in which one animal can learn about a target after it is ensonified by a different animal. Dolphins have been shown to be capable of bistatic sonar in an experiment in which one dolphin clicked at a target and a second dolphin listened to the echoes (Xitco & Roitblat 1996). This second dolphin was able to select the correct target after hearing these echoes. Dolphins can also detect the presence or absence of a target by listening to the echoes of an artificial sound source (Scronce & Johnson 1976).

#### *Differences in the Efficiency of Sonars for Backscatter and Forward Propagation*

When a sonar receiver is removed from the source, this bistatic sonar is not limited to detecting echoes, but can also detect targets if they absorb part of the sonar signal's energy, so-called sound extinction. The bistatic forward propagation mode of sonar operation may offer significant advantages for detecting schools of fish over ranges of many kilometers. Figure 5 diagrams the operation of bistatic sonars where the receiver either detects echoes reflecting back (backscatter mode) or detects extinction in sounds passing through the targets (forward propagation mode). One major difference between these backscatter and forward propagation examples concerns the directionality of echo returns. When sound energy couples to an air bubble, the bubble resonates. This means that the bubble reradiates the sound energy impinging on it in all directions. There is no similar three-dimensional dissipation in the forward

propagation case, with the exception of energy absorbed by the targets. This leads to a large difference in efficiency of the backscatter vs forward modes of sonar operation for these targets. For example, let us compare an omnidirectional sound source used to detect a bubble-like target 100 m away under conditions where sound energy propagates in all directions. As a sound propagates outward in all directions, the sound energy will be distributed over a sphere of radius  $4\pi r^2$ . If you measure the energy at one point at a radius of  $r$  away, the sound energy will be diluted by a ratio of  $1/(4\pi r^2)$  (inverse square law). This is called the spreading loss in underwater acoustics. In the monostatic backscatter case, the sound would dissipate in all directions for the 100 m from the source to the target for a loss of  $1/(4\pi r^2) = 1/(4\pi 100^2)$ . If the bubble then resonates the echo in all directions, there will be a similar loss of  $1/(4\pi 100^2)$  on the return of the echo in the direction of the source. This leads to a total spreading loss of  $1/(4\pi 100^2) \times 1/(4\pi 100^2) = 6 \times 10^{-11}$ . Now let us consider a bistatic sonar using forward propagation in which the receiver is 100 m past the target. In both this and the monostatic backscatter case, the received sound must cover a path length of 200 m, but in the forward propagation mode, a bistatic sonar does not rely upon sound being reradiated from the target. Here the spreading loss is  $1/(4\pi 200^2) = 2 \times 10^{-6}$ , significantly less than in the equivalent monostatic example. The reduced spreading loss is not the only advantage for forward propagation sonar. Theoretical analyses conclude that the target strength of sound absorbed by a gas bubble is greater than the target strength of the backscattered sound (Clay & Medwin 1977).

#### *Sensory Mechanisms Marine Mammals Might Use to Detect Patches of Prey at Ranges of > 1 km*

The above discussion emphasizes the potential utility of low-frequency bistatic sonars for finding patches of fish at ranges of many kilometers. Is this of any relevance to cetaceans? The design features for sonars just discussed for this problem differ markedly from what we know of dolphin echolocation. Research on high-frequency echolocation in dolphins emphasizes its utility in detecting individual targets at ranges up to about 100 m. There is little evidence that it would function well at greater ranges. I am struck by how little attention has been paid to the problem of the sensory mechanisms by which marine mammals orient for navigation and find patches of prey that may be tens to hundreds of meters in size over the range of 1–100 km.

A major problem for foraging cetaceans involves locating evanescent patches of dense prey. Many cetaceans range over 100 kilometers or more per day (e.g., Kruse 1991; Mate 1989), and feed on prey that is highly patchy in time and space. Many toothed whales and dolphins that feed on schooling fish expend considerable energy on the search for prey. For example, dusky dolphins which are feeding primarily on schooling anchovy, swim 5 km/hr in shallow water where they seldom feed, but 16 km/hr in deeper water where they find schools

of anchovy (Würsig & Würsig 1979). These dolphins often spread out in a line perpendicular to their travel and echolocate as they search for prey. If these animals spend much of their travel time searching for food, then any mechanisms to increase the effective range of their biosonar might yield substantial benefits, either in increasing their detections of prey or reducing the energetic cost of searching. Similarly, animals that feed on deep scattering layer organisms could benefit from a biosonar that could detect prey before an animal takes a deep dive.

However, the problem of finding evanescent patches of dense prey is even more acute for baleen whales. Unlike toothed whales which chase individual prey items, baleen whales feed by engulfing an entire mouthful of prey, a volume of hundreds of liters. The denser the concentration of prey in the mouthful, the higher the payoff. Baleen whales are not known to echolocate and nothing is known about the sensory mechanisms by which they find suitably dense patches of prey. There are a few reports of baleen whales establishing small home ranges during the feeding season (Dorsey 1983). However, the enormous scale over which most baleen whales range makes it unlikely that individual whales could find the most productive patches for feeding by local knowledge of a small area. Many baleen whales migrate thousands of kilometers from winter breeding grounds in the tropics in order to take advantage of the burst of productivity in polar waters during the summertime. Most baleen whales are adapted to meet most of their energetic needs for the entire year during this concentrated summer feeding season.

The feeding areas for individuals of some species are very large, comprising thousands of km<sup>2</sup>. For example, in the northwestern Atlantic, a feeding area for humpback whales might comprise the southern Gulf of Maine, or waters from Iceland to Greenland. Within such an area, there are dramatic changes in prey distribution from year to year. Humpback whales feed on schools of prey, either fish such as herring, capelin, and sand lance, or invertebrates including euphausiids such as krill. A newborn humpback calf will follow a mother to her feeding area, and typically will adopt this as its own feeding area. The calf thus has an opportunity for learning general areas of high prey concentration while it is with the mother. However, the calf will wean within its first year of life, and show little later association with the mother. Productive areas for feeding can vary by hundreds of kilometers from year to year. For example, a calf might for its first five years spend most of the feeding season in Stellwagen Bank near Massachusetts, only to find insufficient prey there the sixth year, when it would have to find prey tens or hundreds of kilometers away. Watkins and Schevill (1979) suggest that distant whales may be attracted by the calls of feeding whales. The sensory mechanisms by which whales initially detect either plankton or fish remain little investigated, however. These whales clearly would benefit from mechanisms to detect patches of prey at ranges of tens of kilometers down to meters. Even a crude mechanism that slightly improved a random search could yield high benefits for whales competing for prey.

The optimal prey detector for baleen whales would yield a stronger signal for a larger and denser patch of prey. The data from Weston (1967) and Diachok and Ferla (1996) suggest that a bistatic sonar operating in forward propagation mode at the resonance frequency of swim bladders might detect more attenuation for dispersed prey than for dense schools. This would be suboptimal for detecting the densest schools at the greatest distance. There might be acoustic interactions between the swim bladders of fish in very dense schools, and these would be likely to broaden the bandwidth of the resonance and to lower the resonant frequency compared to single bladders (Clay & Medwin 1977). Whales might be able to assess the density of schools using acoustic features of these interactions between swim bladders. On the other hand, once a whale has detected dispersed prey, it might then be able to use behavioral mechanisms for concentrating dispersed prey. For example, humpback whales will often feed in social groups or emit large bubbles apparently in order to concentrate prey.

#### *Can Cetaceans Use Biosonar in Bistatic or Forward Propagation Mode?*

We have seen the potential utility of low-frequency sonar in a forward propagation mode for finding schools of fish at long ranges and we have also reviewed evidence that some cetaceans face significant problems in finding suitably dense patches of prey at ranges of hundreds or thousands of meters. In particular, the sensory mechanisms by which baleen whales find prey are completely unknown. I would now like to consider the question of whether whales might be able to exploit biosonar in either a forward propagation mode or a bistatic mode or both.

#### *Monostatic Forward Propagation Sonar*

It is possible for an individual cetacean to detect attenuation from fish in a monostatic mode. Recall the earlier discussions about bottom and surface reverberation. Suppose a whale were regularly listening to echoes from these kinds of reverberation. If the path taken by the appropriate sounds were to intersect large patches of fish with swim bladders, then the echoes might sound different than when such targets were not present. The whale might be able to use the attenuation of specific frequencies in the backscattered echo in order to detect prey in the intervening path. As an illustration of the phenomenon I am considering, note the sound from a humpback's song illustrated in Figure 3. This sound was produced during the breeding season away from the feeding grounds, but illustrates the acoustic characteristics of interest. The direct signal from this sound has both an upsweep and a downsweep that pass through the frequency band near 1 kHz at which many fish swim bladders have a resonant frequency. The downsweep has a long section of stable amplitude. If the signal reverberating from the bottom passed through many targets absorbing energy in a narrow

frequency band, then the echo would be likely to have a dropout in that frequency. We do not know much about how large whales hear, but the small toothed whales whose hearing has been tested in captivity have excellent abilities to detect small intensity differences within narrow frequency bands. Bottlenose dolphins can detect frequency differences of 0.2%-0.4% in frequencies between 2 and 53 kHz and differences of 1.4% at 1 and 140 kHz (Jacobs 1972; Herman & Arbeit 1972; Thompson & Herman 1975). Popper (1980) reviews a variety of studies of intensity discrimination and suggests that bottlenose dolphins can probably detect changes in intensity as low as 1 dB. If larger cetaceans have anything like these abilities for intensity discrimination in narrow frequency bands, then they should be quite sensitive to attenuation from fish intervening in the path of their calls.

#### *Bistatic Biosonar*

For the rest of this section I would like to explore the question of whether some cetaceans might be able to use bistatic biosonar. Since marine mammals are highly social and live within the water column, it is possible that they might also use biosonar in a bistatic mode to detect bottom, surface, or volume reverberation. The basic idea behind biological bistatic sonar in a forward propagation mode is that whales might listen for changes in repeated vocalizations of other whales in order to detect targets. A key feature of a bistatic sonar is that the receiver must be able to compare the received signal to a stored representation of the undegraded signal. There are several different mechanisms known for marine mammals that could achieve this end. In order to study possible bistatic sonar, it is necessary to have a method that allows one to follow several individuals, simultaneously recording their vocalizations and behavior. This has only been studied on scales of kilometer separations in a very few situations such as humpback whales on their Hawaiian breeding grounds (Frankel et al. 1995; Tyack 1981) and bowhead whales migrating past Point Barrow, Alaska (Clark et al. 1986).

Bistatic sonar has already been discussed in one of these two cases: the context of bowhead whales sensing reverberation from sea ice. Ellison et al. (1987) present preliminary data suggesting that deep-keeled ice may produce strong echoes from the low-frequency calls of migrating bowhead whales. Clark (1989) and George et al. (1989) suggest that a migrating bowhead whale might use the echoes from the calls of other whales in order to detect an ice obstacle. Würsig and Clark (1993) also specifically discuss the possibility that bowhead whales might use a bistatic sonar in forward propagation mode. When migrating, a bowhead whale will often produce a series of calls with very similar acoustic features, called a signature call. Different migrating bowheads will often counter-call with each individual producing a different signature call (Clark et al. 1986). As Würsig and Clark (1993) describe:

In these counter-calling episodes, one whale calls with its signature call and other whales call with their signature calls within a matter of seconds... these stereotypic calls may allow bowheads to monitor changes in the ice conditions throughout the group's area. In theory, this might be accomplished by comparing the amount of degradation in the stereotypic signals received from another animal. As ice conditions between and around the whales change, the characteristics of the received calls change. (pp. 189-190)

While detection of ice is an important problem for many polar marine mammals, I would like to also discuss the possibility that forward propagation bistatic sonar may have more general utility. For example, I have already discussed how the absorption of sound by swim bladders makes a potential signal for a bistatic biosonar. Let us examine the hypothesis whether cetaceans might listen for frequency-dependent attenuation in order to identify large concentrations of prey fish in the path between caller and receiver. In order for this to work as a bistatic biosonar, the animals would have to produce a series of stereotyped calls. The receiving whale could only identify the frequency-dependent attenuation by comparing the received signal to an expected signal stored in memory. This means that the receiving whale would have to have a clear expectation of what signal will be emitted by the source whale. The receiver could either compare the attenuation at the resonant frequency in successive calls or compare within a call the energy within and outside the frequencies absorbed by the prey. Animals able to make such a comparison, which also searched for food in dispersed groups, would then be able to follow quite simple decision rules in order to close in on a prey patch. For example, countercalling animals might simply swim in parallel when there was no attenuation correlated with prey, but swim toward a calling animal whenever they detected this attenuation.

There have been no studies of vocalizations and foraging behavior in marine mammals that are appropriate for testing the bistatic sonar hypothesis. However, many baleen whales, such as humpback whales, and toothed whales, such as most dolphins and many larger whales such as killer whales, produce calls with energy in the 1 kHz range and feed in groups on fish with swim bladders. I will select killer whales as an example to illustrate a context in which bistatic sonar might function. This species has been selected because we know more about vocalizations during foraging rather than because of any increased expectation they rely upon bistatic sonar.

Killer whales that feed on fish in the Pacific Northwest live in stable social groups, called pods, and they produce echolocation clicks, whistles, and pulsed calls. The pulsed calls separate into discrete and variable calls. The discrete calls can easily be categorized into stable call types while the variable calls cannot be sorted into such well-defined categories (Ford 1989, 1991). Most of the time when these killer whales forage, several pods forage together, suggesting an advantage to increasing group size for foraging. In general, these pods break up during foraging into small subgroups that disperse over areas of several square kilometers (Ford 1989). While dispersed, a foraging killer whale will often



produce a series of the same discrete call, or two or more whales will exchange series of the same call. While all of the pulsed calls are thought to function primarily in social communication, the discrete calls are most associated with foraging and traveling; the more socializing occurring in a group, the higher the abundance of the more variable pulsed calls (Ford 1989).

The top row of Figure 6 shows spectrograms of two discrete calls of these fish-eating killer whales. Each of these calls, N7 and N9, is made up of two sections. The bottom row of Figure 6 shows spectra from the first section of seven different N7 calls on the left and of 12 different N9 calls on the right. These calls were recorded from the same pod but include calls recorded during different sessions. These may include repetitions from the same individual, but probably

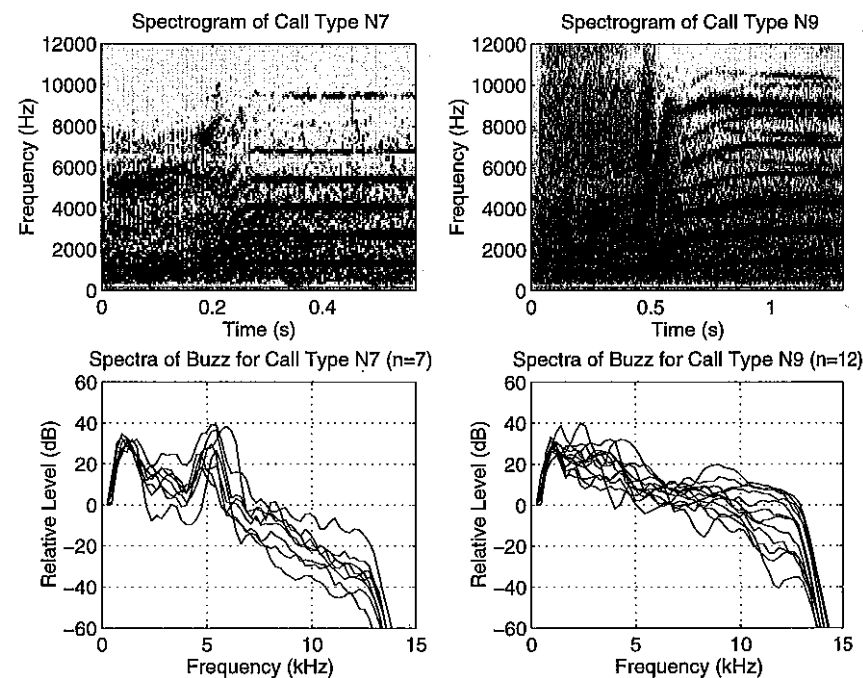


Fig. 6. Illustrations of two kinds of discrete calls made by fish-eating killer whales, *Orcinus orca*, in the Pacific Northwest. Top row: spectrograms of an N7 and an N9 call. Note how each of these calls is made up of two sections. The first section is called a buzz. Bottom row: spectra of the first section of each call. Each figure shows spectra from several calls (bottom left: 7 N7; bottom right: 12 N9) selected from several recording sessions from the A1 pod. Some of these calls may have come from the same individual, but some were likely to have been produced by different individuals from the same group. Each of these calls has relatively low variation in spectra, but the two calls differ in spectra; for example, N7 has a spectral peak near 5 kHz which is absent from N9.

include versions of the same call from different individuals. The spectra of each type of call vary by about  $\pm 5$  dB at any one frequency. Different discrete calls have different spectral maxima. For example the N7 calls illustrated here have a spectral maximum near 5 kHz, while the N9 calls do not.

Whether or not whales could detect fish in the path of the call of another whale depends upon a combination of how precisely they can predict the call structure and by the strength of frequency-dependent attenuation effect from the fish. Stanton (1989) reviews models showing that spherical bubbles have a sharp resonance 37 dB greater than frequencies well above resonance. The Weston (1967) data suggest a 30-dB change in attenuation from simple changes in fish distribution over a very long path length. Diachok and Ferla (1996) report absorption losses of up to 25 dB at the resonance frequencies of sardines over a 12-km path. In order to evaluate the feasibility of bistatic fish-finding biosonar, it will be critical to measure frequency-specific attenuation of sound as a source and receiver separated by several kilometers move from an area with few to many fish prey. If the attenuation effect is on the order of 10–20 dB, then there would be less need for the receiver to have a highly precise internal model of the source's signal. Such attenuation would be obvious given the variance in spectra illustrated in the killer whale calls in Figure 6. More evidence on the spectral stability both of calls within a series produced by one animal and of similar calls between different individuals will be required to evaluate whether stability of call production is consistent with use as a bistatic biosonar signal.

The data just reviewed from killer whales suggest to me that this species has a set of preadaptations for the evolution of bistatic sonar. They feed in groups which disperse when feeding on swim bladder fish, and they share a repertoire of discrete calls that they repeat and exchange while feeding. If their prey caused detectable changes in these signals, then it would be a small step to learn to use this degradation of the signal to learn about the density of prey between signaler and receiver. The fish-eating killer whales of the Pacific Northwest appear to have quite a stable set of prey species such as Pacific salmon (*Oncorhynchus* spp.), rockfish (*Sebastes* spp.) and herring (*Clupea harengus*). Some of these prey, such as rockfish, may not have distribution and behavior suitable for using forward propagation sonar to detect prey patches, while others, such as herring, may be more suitable. If animals capable of high-frequency monostatic sonar, such as killer whales, were to use lower-frequency sounds to detect patches of prey, then one might expect a transition from a low-frequency mode of searching for patches to using higher-frequency sonar for detecting and pursuing individual fish.

If low-frequency signals became adapted for prey detection, then one might expect them to have spectral peaks that match the resonant frequencies of their prey. In the case of killer whales, this might lead to the development of a repertoire of discrete calls that match the resonant frequencies of particular sizes of different prey species.



Killer whales meet the requirements of bistatic sonar by having stable groups in which individuals share stable repertoires of discrete calls. Most other cetacean species have much less stable groups. Long-term memory of stable calls would not be required if cetaceans started calling while together, and continued producing similar calls as they dispersed to search for food. The receiver would not even need to have a representation of the signaler's call if it could make an immediate and precise imitation of a call it heard, whether it was degraded or not. In this case, the original signaler could listen for changes in its original call induced by passage through the water between signaler and receiver and then by passage of the imitated call back from the original receiver to the original sender. This kind of immediate imitation of a call could function in a similar manner to the monostatic forward propagation mode using bottom reverberation discussed in the previous section.

Some of the cetaceans that may feed socially but live in fluid groups are capable of this kind of immediate imitation. Dolphins in captivity can imitate a novel synthetic sound within seconds of the first exposure, which implies a very rapid ability to form at least short-term auditory memories. Dolphins may imitate sounds spontaneously within a few seconds after the first exposure (Herman 1980), or after only a few exposures (Reiss & McCowan 1993).

The ability to learn vocalizations relatively rapidly would not only be useful for animals with fluid groups, but might also allow animals to adapt to rapidly changing prey or noise conditions. For example, humpback whales tend to feed in groups, but these do not tend to have a stable composition of individuals. Humpback whales also appear to be generalists, feeding on a wide variety of prey in many different habitats. We know very little about the vocalizations of humpback whales during the feeding season, but these whales have highly developed abilities to learn the sounds that make up the song during the breeding season. At any one time, the songs of different humpback whales within a population are remarkably similar, yet the song of each individual changes dramatically over time. Sounds may change in duration, frequency, and timbre on a monthly basis; they may disappear from the song entirely, and new sounds may appear in some other part of the song (Payne et al. 1983). Analysis of songs recorded off Bermuda for over two decades showed that once a particular song phrase disappeared, it never recurred (Payne & Payne 1985). The song of each individual is much more like different individuals recorded at the same time than it is to itself recorded, say, a year later (Guinee et al. 1983). This means that all singers change their songs more or less in synchrony over weeks, months, and years. This indicates a powerful selection for vocal convergence to track the long-term changes in the song. There are thus a diversity of mechanisms and time scales over which cetaceans could learn the precise acoustic characteristics of sounds produced by other whales for potential use in a bistatic biosonar.

### *Testing the Bistatic Biosonar Hypothesis*

I have elaborated on speculations about bistatic biosonar in order to generate testable hypotheses about this potential form of biosonar. There are serious limits of purely descriptive studies of feeding in marine mammals. Feeding behavior often appears bewilderingly variable. This probably stems from our ignorance of the actual distribution of prey and of the sensory mechanisms and behavioral strategies employed by the animals in finding, capturing, and handling prey.

Understanding the opportunities afforded to acoustically specialized marine mammals by the physics of ocean acoustics will require close collaborations between underwater acousticians, acoustical oceanographers, and biologists. My own interest in the use of bistatic sonar to detect fish was recently stimulated by recent research of the underwater acoustician Orest Diachok (Diachok 1996; Diachok & Ferla 1996). This exemplifies the importance of close communication between underwater acousticians and biologists interested in how marine animals may use sound. It is difficult enough for humans to have a feel for the sensory world of terrestrial animals. Humans have such limited experience with the underwater world that it is even more difficult to develop an intuitive understanding of the sensory environment of marine animals. This makes it all the more important to rely upon an understanding of the physics of underwater acoustics.

All of the mechanisms for bistatic sonar discussed above would predict that animals would select the signals with spectra that match the absorption spectra of the prey on which they are working at any one time. Underwater acousticians will be able to test both reflected energy and attenuation produced by fish with swim bladders in areas where cetaceans are feeding on fish. If such studies were linked to mapping the distribution of fish, they could verify how useful bistatic biosonar in forward propagation mode might be for detecting fish at ranges that are useful for cetacean feeding. They would also be able to predict expected frequency ranges of optimal sonar signals and to measure the spectra of calls used by cetaceans as they feed on these prey. If descriptive studies were consistent with this biosonar hypothesis, it could be tested using passive acoustic targets. For example, Malme (1994) developed a simple air-filled target that emits no sound but provides a strong echo return from an active sonar. Artificial targets that mimicked the frequency-dependent attenuation of fish swim bladders could enable experimental testing of whether cetaceans do in fact respond to this kind of sonar signal. Whatever the fate of this particular hypothesis, I would argue that progress will come more rapidly with a tighter coupling between natural observations and generation and testing of specific hypotheses on the sensory mechanisms used by foraging cetaceans. Confronting some of the daunting problems solved by marine mammals may also free up our imagination to consider new applications of well-known sensory mechanisms.

Results from testing the bistatic biosonar hypothesis will be interesting whether they are positive or negative. If bistatic biosonar proves to be highly effective for detecting concentrations of fish, and if whales with the appropriate vocal abilities do not in fact use such a system, then this would suggest that abilities evolved for specific communicative purposes may not easily be coopted for the evolution of biosonar abilities. On the other hand, if any cetaceans are demonstrated to use bistatic biosonar in nature, then this would be a fundamentally new form of animal biosonar, one that combines elements of echolocation and of communication.

### PARALLELS BETWEEN ACOUSTIC COMMUNICATION AND ECHOLOCATION

The marine mammal literature tends to assume a rigid dichotomy between echolocation and communication, with high-frequency clicks used exclusively for echolocation and all other sounds used exclusively for social communication. I have discussed how marine mammals may use for biosonar, low-frequency sounds that are typically thought of as serving a communicative function. For example, while humpback song appears to function as a reproductive advertisement display (Tyack 1981), whales may also learn about their environment from listening to echoes of bottom reverberation from sounds used in song. On the other side of this issue, there are also several dolphin species that appear to use "echolocation" clicks for social communication. Several of the species which specialize in high-frequency hearing, including the phocoenid porpoises and dolphins of the genus *Cephalorhynchus* are not known to produce any of the sounds typically associated with social communication in other dolphins (Amundin 1991; Dawson & Thorpe 1990). Both Amundin (1991) and Dawson (1991) suggest that the clicks used in echolocation may also function in social communication. Amundin (1991) associated relatively stereotyped patterns of repetition rate of "echolocation" clicks with specific social contexts. If predators of these species, such as killer whales, cannot hear the high frequencies of these clicks, then it may be advantageous to use them for communication as well as echolocation.

The suggestion that animals may use a bistatic biosonar, where the signaler and receiver are different individuals, further blurs the distinction between communication and echolocation. A phenomenon very similar to bistatic sonar has been discussed by Morton (1982, 1986) in relation to acoustic communication by songbirds. Male songbirds often use song as a territorial display to other males. If a male hears a song within his territory, he ought to respond more strongly than if the song is farther away. Morton has proposed that songbirds estimate the range of a singer by comparing the received song, which has been

degraded by passage through the environment, to a remembered version of the undegraded song. It has been demonstrated that adult male Carolina wrens (*Thryothorus ludovicianus*) respond less to degraded than undegraded song (Richards 1981), and naive young wrens are more likely to learn undegraded than degraded songs (Morton et al. 1986). Great tits (*Parus major*) have also been shown to use this degradation to estimate the distance of a singer, and they are better at estimating the distance of familiar songs than unfamiliar songs (McGregor et al. 1983; McGregor & Krebs 1984). The McGregor and Krebs (1984) results suggest that songbirds need to compare degraded song to an internal representation of an undegraded song in order also to estimate the range of the song of a conspecific. These abilities in great tits are very similar to the ones that marine mammals would need in order to use a bistatic biosonar in forward propagation mode.

Morton (1986) elaborates on this ranging hypothesis by analyzing competitive communication strategies for singing birds and neighbors that use acoustic cues to estimate the range of the song. If territorial neighbors are in competition with one another, then Morton (1986) suggests that selection would favor singers with songs that sounded as close as possible in order to evoke a maximum response at maximum range. The listener on the other hand would be under selection to develop degradation assessment mechanisms that would allow the bird to detect all incursions but to ignore songs from outside of the territory that do not require a response. Morton suggests that large repertoires of complex songs may have evolved in part to interfere with distance assessment mechanisms. Morton also suggests that learning to produce a song may be the best way for a bird to develop a precise auditory representation of that song, and to develop the ability to compare the similarity of auditory input with this auditory memory (following motor theories of sound perception, e.g., Williams & Nottebohm 1985). Morton suggests that the evolution of vocal learning and the tendency of young birds to copy the songs of their neighbors may relate to this arms race between singer and listener concerning distance assessment mechanisms by enhancing the ability of listeners to learn the songs of neighbors.

Morton's evolutionary argument emphasizes the costs and benefits to a signaler for producing a communication signal as well as the costs and benefits to a receiver for ignoring or responding to the signal. This perspective has become common in analyses of animal communication (e.g., Dawkins & Krebs 1978). Myrberg (1981) also emphasizes that signals can be intercepted by unintended receivers, such as predators, to the detriment of the signaler. While interception is usually discussed for communication signals, it also can influence the evolution of echolocation. For example, many insects that are prey for bats have evolved countermeasures against bat biosonar (Miller 1983). Insects can detect the ultrasonic cries of bats and engage in a variety of behavioral strategies to avoid capture including flying away from a distant bat, and diving, falling, or unpredictable zigzag flight away from bats nearby. We know next to nothing

about marine mammal equivalents of the bat-insect arms race, but there are interesting suggestions that interception may be important for marine mammals as well. For example, in the Puget Sound area of the Pacific Northwest, there are two populations of killer whales, *Orcinus orca*. One population feeds on marine mammals, a prey that is sensitive to the frequencies of killer whale clicks; the other population feeds on salmon, a prey that is likely to be much less sensitive. Barrett-Leonard et al. (1996) report that mammal-eating killer whales tend to produce clicks less often than do fish-eating killer whales. When mammal-eating killer whales do click, they vary the intensity, repetition rate, and spectral composition within click trains, apparently making these clicks more difficult for their acoustically sensitive prey to identify than the regular click series of fish-eating killer whales. These results suggest that echolocating whales may modify their echolocation strategy depending upon the auditory sensitivities of their prey. If individual whales can modify their echolocation in this way, this presents parallels with communicative processes in which a signaler modifies its signal depending upon its intended audience (e.g., Marler et al. 1990). Animals producing sounds used by others in a bistatic biosonar mode may also be influenced by the behavior of conspecific receivers.

There is even some suggestive evidence that some fish may be able to intercept high-frequency echolocation sounds of their predators. Some recent research suggests that fish such as alewives (*Alosa pseudoharengus*), herring (*Alosa aestivalis*), and cod (*Gadus morhua*) are able to detect intense sounds of frequencies much higher than is typical of their vocalizations (Astrup & Møhl 1993; Dunning et al. 1992; Nestler 1992). Some of these species are prey for echolocating odontocetes. The only known natural sources of sounds with the intensity and frequency of these ultrasonic stimuli are the clicks of echolocating toothed whales. It is unknown whether this sensitivity happens to be a by-product of an auditory system that evolved to operate at lower frequencies and intensities, or whether fish have evolved an adaptation to enable interception of predators (as was suggested for goldfish by Offutt 1968). Just as the receiver may be a potent source of selection upon a communicative signaler (e.g., Endler 1992; Ryan 1994), so interception of echolocation signals may affect the evolution of hearing in the prey and of echolocation strategies in the echolocating animal.

### Generalized Substrates for the Evolution of Specialized Echolocation Abilities

Pollak (1992) hypothesizes that all higher vertebrates have an ability to perceive echoes and to learn to use echoes for information about their environment. He bases this upon the independent origin of echolocation in animals as diverse as birds, bats, and cetaceans. However, we do not know how important the abilities to process echoes are for animals that have not evolved specialized

high-frequency echolocation. For example, estimation of the elevation angle of a sound may require analysis of reverberation patterns for many animals. For some animals, this may involve reflection from the pinnae and other parts of the body (Kuhn 1987), but animals may also rely upon reflection or reverberation from the environment for estimating the azimuth or elevation of a sound. For example, Berkley (1987) reviews the importance of reverberation in rooms for sound localization by humans. Predictably reflective surfaces such as the sea surface might present similar opportunities for marine organisms. Sound localization may select for auditory processing skills that could then play a role in the evolution of more specialized forms of echolocation. For example, if animals rely upon interaural time delays to locate a sound, might these abilities for precise timing of sounds also be used for timing delays between signal and echo? Some of the initial stages in the evolution of specialized high-frequency biosonar may have evolved from the use of more generalized auditory abilities to solve simple biosonar tasks such as those I suggest for low-frequency signals. In this essay I have suggested factors that may have affected the evolution of echolocation abilities in marine mammals. There has been little examination of how much cetaceans were able to recruit general mammalian auditory abilities for echolocation vs requiring the evolution of more specialized audition, beyond their obvious abilities for more rapid processing of higher frequencies.

Psychologists have debated for decades about the relative importance of general vs specialized learning abilities. For example, some linguists have argued that perception of speech involves a highly specialized "module" that shares little information or central mechanisms with a module, say, for the perception of music (e.g., Fodor 1983). Some students of animal intelligence have argued in a similar vein that cognitive skills used by animals in social interactions may not generalize to nonsocial contexts (Cheney & Seyfarth 1990). Most students of biosonar and acoustic communication appear to assume implicitly that the use of sound to explore the inanimate environment involves a module completely independent from that used to communicate acoustically with conspecifics. I would like to suggest that this is an untested hypothesis and should be evaluated more explicitly.

### *Learning Mechanisms for Matching Biosonar or Communication Signals to Local Circumstances*

Some species appear to have evolved mechanisms for vocal production that involve signals that cannot be modified by auditory input. However, many sonar and communication problems require modification of the outgoing signal depending upon the auditory environment. A simple example common to both sonar and communication involves switching output frequency to avoid jamming by another source operating at the same frequency. This ability to modify one's vocal output depending upon auditory input is called vocal learning. Vocal

learning is critical for the development of human communication, and its benefits are so obvious that it is surprising to find that it is rare among animals.

Most animals appear to have mechanisms for patterning vocal signals that are remarkably resistant to modification. Even such drastic treatments as deafening at birth, which would derail vocal development in humans and many bird species, do not prevent terrestrial nonhuman mammals from developing normal vocalizations (e.g., Buchwald & Shipley 1985). Primates raised in isolation or with foster mothers of a different species still produce species-typical vocalizations even though these animals are constantly exposed to, and must learn to respond to, vocalizations that differ from the ones they produce themselves (Owren et al. 1993; Winter et al. 1973).

Kroodsma and Konishi (1991) suggest that vocal learning requires special neural connections between auditory input and vocal motor output, connections that are present in songbird species that learn their song, but that appear absent in bird species that do not learn their song. Discussions of the evolution of vocal learning in birds and mammals tend to emphasize the importance of communication. However, echolocation also requires the ability to modify one's vocal output depending upon what one hears. Animals with short echolocation pulses at the very least emit pulses so they do not overlap with incoming echoes. Bats that perform Doppler compensation modify their outgoing signal to maintain the appropriate frequency of the echo. Neural connections between auditory input and vocal motor output have also been reported for several bat species (Covey & Casseday 1995). This raises the question whether connections between auditory input and vocal output are limited to either a communicative or sonar function, or whether they may have more general functionality.

If these kinds of connections create the potential for general abilities of vocal learning, and if vocal learning plays important roles in either communication or echolocation, then the evolution of vocal learning for echolocation may preadapt animals to be able to use the abilities for communication, or vice versa. There are hints of evolutionary interactions between these two functions for vocal learning. Both echolocation and the ability to modify communication signals based upon auditory input are rare among animals, but both abilities tend to occur in the same taxa of animals. For example, the only nonhuman mammals for which there is evidence for vocal learning are bats (e.g., Jones & Ransome 1993) and marine mammals (e.g., Tyack & Sayigh 1997), and these are also our best examples of animal echolocation. Vocal learning in bats has been described both for sounds used in echolocation (Jones & Ransome 1993) and communication (Esser & Schmidt 1989). Vocal learning is well known for communication signals in whales and dolphins, and beluga whales are known to modify the frequency structure of their echolocation clicks depending upon ambient noise (Au et al. 1985).

Discussions of vocal learning tend to focus simply upon matching vocal output to auditory input. Most other forms of learning are linked to some more

extrinsic reinforcement. West and King (1990) suggest that some birds may direct their vocal development by creating a diverse array of sounds and then selecting which sounds they repeat depending upon the social responses evoked by their sounds. For example, West and King (1990) studied starlings (*Sturnus vulgaris*) which are accomplished mimics. Starlings raised by humans imitate many sounds in their environment. These birds are particularly likely to produce excellent imitations of the sounds of humans with whom they interact. The only starlings to imitate human sounds were those that interacted with humans on a regular basis. West and King (1990) suggest that it is this social interaction that enables these birds to shape their vocalizations to produce such excellent imitations of human speech while ignoring socially irrelevant sounds such as the dishwasher. This vocal learning does not just involve matching vocal output to auditory input, but must also involve social reinforcement as well. These birds imitate speech so precisely that they must not only select preexisting sounds but to modify the sounds and slowly shape their vocal repertoire depending upon the responses which these modifications evoke.

West and King (1988) provide evidence that this kind of nonvocal behavioral feedback between conspecifics may also direct vocal development in more natural circumstances. Male cowbirds will modify the songs they sing depending upon how likely the sounds are to elicit distinctive wing movements from female cowbirds. West and King (1990) also suggest analogies between communicative and echolocation in describing the open system for vocal development involving social feedback:

We propose that some birds use acoustic probes to test the contingent properties of their environment, an interpretation largely in keeping with concepts of communication as processes of social negotiation and manipulation. An analogy with the capacities of echo-locating animals may be appropriate. Like bats or dolphins emitting sounds to estimate distance, some birds may bounce sounds off the animate environment, using behavioral reverberations to gauge the effects of their vocal efforts. (p. 113)

Many marine mammals also have exceptional skills of vocal imitation. Captive bottlenose dolphins of both sexes are highly skilled at imitating synthetic pulsed sounds and whistles (Caldwell & Caldwell 1972; Evans 1967; Richards et al. 1984). A captive harbor seal, *Phoca vitulina*, was reported to imitate human speech with a regional accent (Ralls et al. 1985). Captive beluga whales, *Delphinapterus leucas*, are also reported to imitate human speech well enough for caretakers to "perceive these sounds as emphatic human conversation" (Ridgway et al. 1985) or even for words to be recognized (Eaton 1979). The songs of humpback whales, *Megaptera novaeangliae*, are very similar within a population but change progressively over time (Payne et al. 1983). The vocal convergence at any one time within a population of singing humpback whales coupled with the rapid changes in the song over time provide evidence for vocal matching in these animals. Both the evolutionary origins and current utility of these imitative skills in marine mammals remain obscure.

West and King (1990) focus upon the extraordinary flexibility of vocal development that proceeds by comparing production of an arbitrary sound with the communicative benefit of using that sound. The same general abilities for vocal learning and flexibility in vocal development might also enable animals to use sound to explore their inanimate environment. For example, even though humans do not have specialized echolocation abilities, both blind and sighted humans can detect, locate, and discriminate targets by listening to echoes (Rice 1969). Learning and practice can enhance these general abilities to use echoes. If humans are allowed to spend an hour or so trying out their own vocalizations to find one that yields good echo information, their performance with this signal is about as good as that with artificial signals designed for enhancing echoes.

Humans appear to have evolved vocal learning for the communication, but we can also use this skill to rapidly learn signals that can help us explore our environment acoustically. Animals with biosonar abilities as highly evolved as the communicative abilities of the starling may also derive benefit from an open system of vocal development in which the feedback for vocal learning derives from the utility of different sounds for exploring the environment. Once evolved for biosonar, an open system of vocal development might also facilitate the development of communicative skills. Most biologists tend to think of sonar and communication as involving distinctly separate central mechanisms. The open process of vocal development described by West and King (1988, 1990) suggests the possibility that a more generalized skill might function to hone either communicative or biosonar skills. Animals that use vocal learning to modify sounds used for echolocation and sounds used for communication, such as bats and marine mammals, are particularly interesting candidates for testing the interplay between highly specialized and canalized skills vs more open and general mechanisms in learning and development.

## ACKNOWLEDGMENTS

I started thinking about this essay during a year at the Center for Advanced Study in the Behavioral Sciences in Stanford, CA. Thanks to the Center for an excellent environment to develop new ideas. Support was provided by a Mellon Independent Study Award from the Woods Hole Oceanographic Institution and from NSF grant #SBR-9022192 to the Center for Advanced Study in the Behavioral Sciences. I would like to thank Christopher Clark, Orest Diachok, Kurt Fristrup, Donald Griffin, Vincent Janik, Cynthia Moss, Donald Owings, and Nicholas Thompson for comments on an earlier version of this chapter. Thanks to Orest Diachok and David Farmer for informal discussions about the forward propagation mode of bistatic sonar, particularly with respect to fish with swim bladders as targets. I must take responsibility for any errors in my description of

the underwater acoustics or in my extrapolations to bioacoustics, but I would like to credit Diachok with suggesting the utility of a bistatic mode of biosonar to detect fish over large ranges of kilometers or more. The recordings of sperm whales came from research cruises in the Caribbean with Dr. William A. Watkins. Thanks to Patrick Miller for providing the data used for Figure 6 and to Patrick Miller and Pamela Willis for help producing the figures. Don Griffin suggested the idea of a monostatic biosonar using echoes from bottom reverberation to operate in forward propagation mode. This is contribution number 9246 from the Woods Hole Oceanographic Institution.

## REFERENCES

- Amundin, M. (1991). Click repetition rate patterns in communicative sounds from the harbour porpoise, *Phocoena phocoena*. Chapter in Ph.D. thesis, Sound production in odontocetes with emphasis on the harbour porpoise, *Phocoena phocoena*, University of Stockholm
- Astrup, J., Möhl, B. (1993). Detection of intense ultrasound by the cod *Gadus morhua*. *J Exp Biol* 182:71-80
- Au, W. W. L. (1980). Echolocation signals of the Atlantic bottlenose dolphin (*Tursiops truncatus*) in open waters. In: Busnel R-G, Fish JF (eds) *Animal sonar systems*, New York: Plenum, pp 251-282
- Au, W. W. L. (1993). *The sonar of dolphins*. New York: Springer
- Au, W. W. L., Carder, D. A., Penner, R. H., Scronce, B. L. (1985). Demonstration of adaptation in beluga whale echolocation signals. *J Acoust Soc Am* 77:726-730
- Au, W. W. L., Pawloski, J. L., Nachtigall, P. E., Blonz, M., Gisinger, R. C. (1995). Echolocation signals and transmission beam pattern of a false killer whale (*Pseudorca crassidens*). *J Acoust Soc Am* 98:51-59
- Backus, R., Schevill, W. E. (1962). *Physeter* clicks. In: Norris KS (ed) *Whales, dolphins, and porpoises*. Berkeley: University of California Press, pp 510-528
- Barrett-Lennard, L. G., Ford, J. F. B., Heise, K. A. (1996). The mixed blessing of echolocation: differences in sonar use by fish-eating and mammal-eating killer whales. *Anim Behav* 51:553-565
- Batzler, W. E., Pickwell, G. V. (1970). Resonant acoustic scattering from gas-bladder fish. In: Farquhar GB (ed) *Proceedings of an international symposium on biological sound scattering in the ocean*. Washington DC: Govt Printing Office.
- Berkley, D. A. (1987). Hearing in rooms. In: Yost WA, Gourevitch G (eds) *Directional hearing*. New York: Springer, pp 249-260
- Bodenhamer, R. D., Pollak, G. D. (1983). Response characteristics of single units in the inferior colliculus of mustache bats to sinusoidally frequency modulated signals. *J Comp Physiol* 153:67-79
- Braham, H. W., Fraker, M. A., Krogman, B. D. (1980). Spring migration of the Western Arctic population of bowhead whales. *Mar Fish Rev* 42:36-46
- Brill, R. L., Pawloski, J. L., Helweg, D. A., Au, W. W., Moore, P. W. B. (1992). Target detection, shape discrimination, and signal characteristics of an echolocating false killer whale (*Pseudorca crassidens*). *J Acoust Soc Am* 92:1324-1330
- Buchwald, J. S., Shipley, C. (1985). A comparative model of infant cry. In: Lester BM, Boukydis CFZ (eds) *Infant crying*. New York: Plenum, pp 279-305

- Busnel, R.-G., Dzedzic, A. (1966). Acoustic signals of the pilot whale, *Globicephala melaena* and of the porpoises *Delphinus delphis* and *Phocoena phocoena*. In: Norris KS (ed) *Whales, dolphins, and porpoises*. Berkeley: University of California Press, pp 607–646
- Caldwell, M. C., Caldwell, D. K. (1967). Intraspecific transfer of information via the pulsed sound in captive odontocete cetaceans. In: Busnel R-G (ed) *Animal Sonar Systems*. NATO Advanced Study Institute, Jouy-en-Josas: Laboratoire de physiologie acoustique, vol 2, pp 879–936
- Caldwell, M. C., Caldwell, D. K. (1972). Vocal mimicry in the whistle mode by an Atlantic bottlenosed dolphin. *Cetology* 9:1–8
- Cheney, D. L., Seyfarth, R. M. (1990). *How monkeys see the world*. Chicago: University of Chicago Press
- Clapham, P. J., Mattila, D. K. (1990). Humpback whale songs as indicators of migration routes. *Marine Mammal Science* 6:155–160
- Clark, C. W. (1989). The use of bowhead whale call tracks based on call characteristics as an independent means of determining tracking parameters. *Rep Int Whal Comm* 39:111–113
- Clark, C. W. (1993). Bioacoustics of baleen whales: from infrasonics to complex songs. *J Acoust Soc Am* 94:1830, Abstract
- Clark, C. W., Ellison, W. T., Beeman, K. (1986). Acoustic tracking of migrating bowhead whales. *Proceedings of the IEEE Oceans 86 Conference* 86:341–346
- Clay, C. S., Medwin, H. (1977). *Acoustical oceanography*. New York: Wiley
- Covey, E., Casseday, J. H. (1995). The lower brainstem auditory pathways. In A. N. Popper & R. R. Fay (Eds.), *Hearing by bats*. New York: Springer, pp 235–295
- Curran, T. A., Lemon, D., Ye, Z. (1994). The acoustic scintillation flowmeter: application for a new environmental tool. *Journal of the Canadian Hydrographic Association* 49:25–29.
- Dawkins, R., Krebs, J. R. (1978). Animal signals: information or manipulation? In J. R. Krebs & N. B. Davies (Eds.), *Behavioural ecology*. Oxford: Blackwell, pp 282–309
- Dawson, S., Thorpe, C. W. (1990). A quantitative analysis of the sounds of Hector's dolphin. *Ethology* 86:131–145
- Dawson, S. (1991). Clicks and communication: the behavioral and social contexts of Hector's dolphin vocalizations. *Ethology* 88: 265–276.
- Diachok, O. (1996). Fish absorption spectroscopy. In J. Papadakis (Ed.), *Proceedings of the third European conference on underwater acoustics*. Luxembourg: EC Press
- Diachok, O., Ferla, C. (1996). Measurement and simulation of the effects of absorptivity due to fish on transmission loss in shallow water. *Oceans 96 Conference Proceedings*, Piscataway NJ: IEEE Service Center
- Dorsey, E. M. (1983). Exclusive adjoining ranges in individually identified minke whales (*Balaenoptera acutorostrata*) in Washington state. *Can J Zool* 61:174–181
- Dudok, van Heel, W. H. (1981). Investigations on cetacean sonar. III. A proposal for an ecological classification of cetaceans in relation to sonar. *Aquatic Mammals* 8:65–68
- Dunning, D. J., Ross, Q. E., Geoghegan, P., Reichle, J. J., Menezes, J. K., Watson, J. K. (1992). Alewives avoid high-frequency sound. *North American Journal of Fisheries Management* 12:407–416
- Eaton, R. L. (1979). A beluga whale imitates human speech. *Carnivore* 2:22–23
- Ellison, W. T., Clark, C. W., Bishop, G. C. (1987). Potential use of surface reverberation by bowhead whales, *Balaena mysticetus*, in under-ice navigation. *Rep Int Whal Comm* 37:329–332
- Endler, J. A. (1992). Signals, signal conditions, and the direction of evolution. *Am Nat* 139S:S125–S153
- Esser, K.-H., Schmidt, U. (1989). Mother-infant communication in the lesser spear-nosed bat, *Phyllostomus discolor* (Chiroptera, Phyllostomatidae) — evidence for acoustic learning. *Ethology* 82:156–168

- Evans, W. E. (1967). Vocalization among marine mammals. In: Tavolga WN (ed) *Marine bioacoustics*. Oxford: Pergamon, vol 2, pp 159–186
- Evans, W. E., Awbrey, F. T., Hackbarth, H. (1988). High frequency pulse produced by free ranging Commerson's dolphin *Cephalorhynchus commersonii* compared with those of phocoenids. *Rep Int Whal Comm Special Issue* 9:173–181
- Fenton, M. B. (1995). Natural history and biosonar signals. In A. N. Popper & R. R. Fay (Eds.), *Hearing by bats*. New York: Springer, pp 37–86
- Fletcher, S., Le Boeuf, B. J., Costa, D. P., Tyack, P. L., Blackwell, S. B. (1996). Onboard acoustic recording from diving northern elephant seals. *J Acoust Soc Am* 100:2531–2539
- Fodor, J. A. (1983). *The modularity of mind*. Cambridge: MIT Press
- Ford, J. K. B. (1989). Acoustic behavior of resident killer whales (*Orcinus orca*) off Vancouver Island, British Columbia. *Can J Zool* 67:727–745
- Ford, J. K. B. (1991). Vocal traditions among resident killer whales (*Orcinus orca*) in coastal waters of British Columbia. *Can J Zool* 69:1454–1483
- Frankel, A. S., Clark, C. W., Herman, L. M., Gabriele, C. M. (1995). Spatial distribution, habitat utilization, movements, and social interactions of humpback whales, *Megaptera novaeangliae*, off Hawaii using acoustic and visual techniques. *Can J Zool* 73:1134–1136
- George, J. C., Clark, C., Carroll, G. M., Ellison, W. T. (1989). Observations on the ice-breaking and ice navigation behavior of migrating bowhead whales (*Balaena mysticetus*) near Point Barrow, Alaska, spring 1985. *Arctic* 42:24–30
- Griffin, D. R. (1955). Hearing and acoustic orientation in marine animals. *Deep-Sea Research, supplement* to 3:406–417
- Griffin, D. R. (1974). *Listening in the dark*. New York: Dover
- Griffin, D. R. (1980). Early history of research on echolocation. In: Busnel R-G, Fish JF (eds) *Animal sonar systems*. New York: Plenum, pp 1–8
- Grinnell, A. D. (1995). Hearing in bats: an overview. In: Popper AN, Fay RR (eds) *Hearing by bats*. New York: Springer, pp 1–36
- Guinee, L., Chu, K., Dorsey, E. M. (1983). Changes over time in the songs of known individual humpback whales (*Megaptera novaeangliae*). In R. Payne (Ed.), *Communication and behavior of whales*. Boulder: Westview Press
- Harvey, P. H., Pagel, M. D. (1991). *The comparative method in evolutionary biology*. Oxford: Oxford University Press
- Hatakeyama, Y., Soeda, H. (1990). Studies on echolocation of porpoises taken in salmon gillnet fisheries. In J. A. Thomas & R. Kastelein (Eds.), *Sensory abilities of cetaceans*. New York: Plenum, pp 269–281
- Herman, L. M. (1980). The communication systems of cetaceans. In L. M. Herman (Ed.), *Cetacean behavior: mechanisms and functions*. New York: Wiley-Interscience, pp 149–209
- Herman, L. M., Arbeit, W. R. (1972). Frequency discrimination limens in the bottlenosed dolphin: 1–70 KC/S. *J Aud Res* 2:109–120
- Hersey, J. B., Backus, R. H. (1962). Sound scattering by marine organisms. In M. N. Hill (Ed.), *The sea*. New York: Interscience Publishers, vol 1, pp 498–539
- Horton, J. W. (1959). *Fundamentals of sonar*. Annapolis: United States Naval Institute
- Hui, C. A. (1994). Lack of association between magnetic patterns and the distribution of free-ranging dolphins. *J Mammal* 75:399–405
- Hunt, F. V. (1954). *Electroacoustics*. New York: Wiley and Harvard University Press
- Jacobs, D. W. (1972). Auditory frequency discrimination in the Atlantic bottlenose dolphin *Tursiops truncatus* Montagu: a preliminary report. *J Acoust Soc Am* 52:696–698
- Jones, G., Ransome, R. D. (1993). Echolocation calls of bats are influenced by maternal effects and change over a lifetime. *Proc Roy Soc Lond B* 252:125–128
- Kamminga, C. (1988). Echolocation signal types of odontocetes. In P. E. Nachtigall & P. W. B. Moore (Eds.), *Animal sonar: processes and performance*. New York: Plenum, pp 9–22



- Kamminga, C., Wiersma, H. (1981). Investigations on cetacean sonar II. Acoustical similarities and differences in odontocete sonar signals. *Aquatic Mammals* 8:41-62
- Kamminga, C., Wiersma, H. (1982). Investigations on cetacean sonar V. The true nature of the sonar sound of *Cephalorhynchus commersonii*. *Aquatic Mammals* 9:95-104
- Kellogg, W. N. (1961). *Porpoises and sonar*. Chicago: University of Chicago Press.
- Ketten, D. R. (1994). Functional analyses of whale ears: adaptations for underwater hearing. *IEEE Proceedings in Underwater Acoustics* 1:264-270
- Kick, S. A., Simmons, J. A. (1984). Automatic gain control in the bat's sonar receiver and the neuroethology of echolocation. *J Neurosci* 4:2725-2737
- Kinne, O. (1975). *Marine ecology*. London: Wiley, volume 2, part 2
- Klinowska, M. (1985). Cetacean live stranding dates relate to geomagnetic disturbances. *Aquatic Mammals* 11:109-119
- Kroodtsma, D., Konishi, M. (1991). A subsong bird (eastern phoebe, *Sayornis phoebe*) develops song without auditory feedback. *Anim Behav* 42:477-487
- Kruse, S. (1991). The interactions between killer whales and boats in Johnstone Strait, B.C. In K. Pryor & K. S. Norris (Eds.), *Dolphin societies*. Berkeley: University of California Press, pp 149-159
- Kuhn, G. F. (1987). Physical acoustics and measurements pertaining to directional hearing. In W. A. Yost & G. Gourevitch (Eds.), *Directional hearing*. New York: Springer, pp 3-25
- Le Boeuf, B. J., Costa, D. P., Huntley, A. C., Feldcamp, S. D. (1988). Continuous deep diving in female northern elephant seals, *Mirounga angustirostris*. *Can J Zool* 66:446-458
- Le Boeuf, B. J., Laws, R. M. (1994). *Elephant seals*. Berkeley: University of California Press
- Love, R. H. (1973). Target strengths of humpback whales *Megaptera novaeangliae*. *J Acoust Soc Am* 54:1312-1315
- Malme, C. I. (1994). Development of a high target strength passive acoustic reflector for low-frequency sonar applications. *IEEE J Oceanic Eng* 19:438-448
- Marler, P., Karakashian, S., Gyger, M. (1990). Do animals have the option of withholding signals when communication is inappropriate? In C. A. Ristau (Ed.), *Cognitive ethology: The minds of other animals* (essays in honor of Donald R Griffin). Hillsdale, NJ: Erlbaum
- Marten, K., Norris, K. S., Moore, P. W. B., Englund, K. A. (1988). Loud impulse sounds in odontocete predation and social behavior. In P. E. Nachtigall & P. W. B. Moore (Eds.), *Animal sonar: processes and performance*. New York: Plenum, pp 567-579
- Martin, A. R. (1995). How do whales find the next breathing site when travelling under heavy sea-ice? In: *Abstracts, Eleventh Biennial Conference on the Biology of Marine Mammals*, p 73
- Mate, B. (1989). Satellite monitored radio tracking as a method for studying cetacean movements and behavior. *Rep Int Whal Comm* 39:389-391
- McDonald, M. A., Hildebrand, J. A., Webb, S. C. (1995). Blue and fin whales observed on a seafoor array in the Northeast Pacific. *J Acoust Soc Am* 98:712-721
- McGregor, P. K., Krebs, J. R. (1984). Sound degradation as a distance cue in great tit (*Parus major*) song. *Behav Ecol Sociobiol* 16:49-56
- McGregor, P. K., Krebs, J. R., Ratcliffe, L. M. (1983). The response of great tits (*Parus major*) to the playback of degraded and undegraded songs: the effect of familiarity with the stimulus song type. *Auk* 100:898-906
- Menne, D., Kaipf, I., Wagner, I., Ostwald, J., Schnitzler, H.-U. (1989). Range estimation by echolocation in the bat *Eptesicus fuscus*: trading of phase versus time cues. *J Acoust Soc Am* 85:2642-2650
- Miller, L. A. (1983). How insects detect and avoid bats. In F. Huber & H. Markl (Eds.), *Neuroethology and behavioral physiology: roots and growing pains*. New York: Springer
- Moore, P. W. B. (1980). Cetacean obstacle avoidance. In: Busnel R-G, Fish JF (eds) *Animal sonar systems*. New York: Plenum, pp 97-108

- Moore, P. W. B., Pawloski, D. (1991). Investigation on the control of echolocation pulses in the dolphin (*Tursiops truncatus*). In J. Thomas & R. Kastelein (Eds.), *Sensory abilities of cetaceans*. New York: Plenum, pp 305-316
- Morton, E. S. (1982). Grading, discreteness, redundancy, and motivation-structural rules. In D. E. Kroodtsma & E. H. Miller (Eds.), *Acoustic communication in birds*. New York: Academic Press, vol 1, pp 183-212
- Morton, E. S. (1986). Predictions from the ranging hypothesis for the evolution of long distance signals in birds. *Behaviour* 99:65-86
- Morton, E. S., Gish, S. L., van der Voort, M. (1986). On the learning of degraded and undegraded songs in the Carolina wren. *Anim Behav* 34:815-820
- Murchison, A. E. (1980). Detection range and range resolution of echolocating bottlenose porpoise (*Tursiops truncatus*). In R.-G. Busnel & J. F. Fish (Eds.), *Animal sonar systems*. New York: Plenum, pp 43-70
- Myrberg, A. A., Jr. (1981). Sound communication and interception in fishes. In W. N. Tavolga, A. N. Popper & R. R. Fay (Eds.), *Hearing and sound communication in fishes*. New York: Springer
- Nestler, J. M., Ploskey, G. R., Pickens, J., Menezes, J., Schilt, C. (1992). Responses of blueback herring to high-frequency sound and implications for reducing entrainment at hydropower dams. *North American Journal of Fisheries Management* 12:667-683
- Neuweiler, G. (1990). Auditory adaptations for prey capture in echolocating bats. *Physiol Rev* 70:615-641
- Neuweiler, G., Link, A., Marimuthu, G., Rübtsamen, R. (1988). Detection of prey in echoclouding environments. In P. E. Nachtigall & P. W. B. Moore, (Eds.), *Animal sonar: processes and performance*. New York: Plenum, pp 613-618
- Norris, K. S. (1967). Some observations on the migration and orientation of marine mammals. In R. M. Storm (Ed.), *Animal orientation and navigation*. Corvallis: Oregon State University Press
- Norris, K. S. (1969). The echolocation of marine mammals. In H. T. Andersen (Ed.), *The biology of marine mammals*. New York: Academic Press
- Norris, K. S. (1974). *The porpoise watcher*. New York: Norton
- Norris, K. S., Möhl, B. (1983). Can odontocetes debilitate prey with sound? *Am Nat* 122:85-104
- Offut, C. G. (1968). Auditory response in the goldfish. *J Aud Res* 8:391-400
- Owren, M. J., Dieter, J. A., Seyfarth, R. M., Cheney, D. L. (1993). Vocalizations of rhesus (*Macaca mulatta*) and Japanese (*Macaca fuscata*) macaques cross-fostered between species show evidence of only limited modification. *Developmental Psychobiology* 26:389-406
- Pack, A. A., Herman, L. M. (1995). Sensory integration in the bottlenosed dolphin: immediate recognition of complex shapes across the senses of echolocation and vision. *J Acoust Soc Am* 98:722-733
- Papastavrou, V., Smith, S. C., Whitehead, H. (1989). Diving behaviour of the sperm whale, *Physeter macrocephalus*, off the Galapagos Islands. *Can J Zool* 67:839-846
- Papi, F. (1992). *Animal homing*. New York: Chapman and Hall
- Parsons, T. R., Takahashi, M., Hargrave, B. (1984). *Biological oceanographic processes*. Oxford: Pergamon
- Payne, K., Payne, R. (1985). Large scale changes over 19 years in the songs of humpback whales in Bermuda. *Zeitschrift für Tierpsychologie* 68:89-114
- Payne, K. B., Tyack, P., Payne, R. S. (1983). Progressive changes in the songs of humpback whales. In R. S. Payne (Ed.), *Communication and behavior of whales*. AAAS Selected Symposia Series. Boulder: Westview Press, pp 9-59
- Payne, R. S., Webb, D. (1971). Orientation by means of long range acoustic signalling in baleen whales. *Ann NY Acad Sci* 188:110-141
- Pike, G. (1962). Migration and feeding of the grey whale (*Eschrichtius gibbosus*). *J Fish Res Board Can* 19:815-838

- Pollak, G. D. (1992). Adaptations of basic structures and mechanisms in the cochlea and central auditory pathway of the mustache bat. In A. N. Popper, R. R. Fay, & D. B. Webster (Eds.), *Evolutionary biology of hearing*. New York: Springer, pp 751–778
- Popper, A. N. (1980). Sound emission and detection by delphinids. In L. M. Herman (Ed.), *Cetacean behavior: mechanisms and functions*. New York: Wiley-Interscience, pp 1–52
- Ralls, K., Fiorelli, P., Gish, S. (1985). Vocalizations and vocal mimicry in captive harbor seals, *Phoca vitulina*. *Can J Zool* 63:1050–1056
- Reiss, D., McCowan, B. (1993). Spontaneous vocal mimicry and production by bottlenose dolphins (*Tursiops truncatus*): evidence for vocal learning. *J Comp Psychol* 107:301–312
- Renaud, D. L., Popper, A. N. (1975). Sound localization by the bottlenose porpoise, *Tursiops truncatus*. *J Exp Biol* 63:569–585
- Rice, C. E. (1969). Perceptual enhancement in the early blind? *The Psychological Record* 19:1–14
- Richards, D. G. (1981). Estimation of distance of singing conspecifics by the Carolina wren. *Auk* 98:127–133
- Richards, D. G., Wolz, J. P., Herman, L. M. (1984). Vocal mimicry of computer-generated sounds and vocal labeling of objects by a bottlenosed dolphin, *Tursiops truncatus*. *J Comp Psychol* 98:10–28
- Ridgway, S. H., Carder, D. A., Jeffries, M. M. (1985). Another “talking” male white whale. *Abstracts, Sixth Biennial Conference on the Biology of Marine Mammals*, p 67
- Ryan, M. J. (1994). Mechanisms underlying sexual selection. In L. A. Real (Ed.), *Behavioral mechanisms in evolutionary ecology*. Chicago: University of Chicago Press, pp 190–215
- Schmidt-Koenig, K. (1975). *Migration and homing in animals*. New York: Springer
- Schnitzler, H.-U. (1968). Die Ultraschall-Ortungslaute der Hufeisen Fledermäuse (Chiroptera-Rhinolophidae) in verschiedenen Orientierungssituationen. *Z vergl Physiol* 57:376–408
- Schnitzler, H.-U., Ostwald, J. (1983). Adaptation for the detection of fluttering insects by echolocation in horseshoe bats. In J. P. Ewert, R. R. Capranica, D. J. Ingle (Eds.), *Advances in vertebrate neuroethology*. New York: Plenum, pp 801–827
- Schuller, G., Beuter, K., Schnitzler, H.-U. (1974). Responses to frequency shifted artificial echoes in the bat, *Rhinolophus ferrumequinum*. *J Comp Physiol A* 89:275–286
- Schuller, G., Pollak, G. D. (1979). Disproportionate frequency representation in the inferior colliculus of Doppler-compensating greater horseshoe bats: evidence for an acoustic fovea. *J Comp Physiol A* 132:47–54
- Schusterman, R. J. (1972). Visual acuity in pinnipeds. In H. E. Winn, & B. L. Olla (Eds.), *Behavior of marine animals*. New York: Plenum, vol 2, pp 469–492
- Schusterman, R. J. (1981). Behavioral capabilities of seals and sea lions: a review of their hearing, visual learning and diving skills. *The Psychological Record* 31:125–143
- Scronce, B. L., Johnson, C. S. (1976). Bistatic target detection by a bottlenosed porpoise. *J Acoust Soc Am* 59:1001–1002
- Simmons, J. A., Ferragamo, M. J., Saillant, P. A., Haresign, T., Wotton, J. M., Dear, S. P., Lee, D. N. (1995). Auditory dimensions of acoustic images in echolocation. In A. N. Popper, R. R. Fay (Eds.), *Hearing by bats*. New York: Springer
- Simmons, J. A., Kick, S. A. (1983). Interception of flying insects by bats. In F. Huber, H. Markl (Eds.), *Behavioral physiology and neuroethology: roots and growing points*. New York: Springer
- Stanton, T. K. (1989). Simple approximate formulas for backscattering of sound by spherical and elongated objects. *J Acoust Soc Am* 86:1499–1510
- Thompson, R. K. R., Herman, L. M. (1975). Underwater frequency discrimination in the bottlenosed dolphin (1–140 kHz) and human (1–8 kHz). *J Acoust Soc Am* 57:943–948
- Thompson, T. J., Winn, H. E., Perkins, P. J. (1979). Mysticete sounds. In H. E. Winn, B. L. Olla (Eds.), *Behavior of marine animals*. New York: Plenum, vol 3, pp 403–431
- Turl, C. W., Penner, R. H. (1989). Differences in echolocation click patterns of the beluga (*Delphinapterus leucas*) and the bottlenose dolphin (*Tursiops truncatus*). *J Acoust Soc Am* 86:497–502

- Tyack, P. (1981). Interactions between singing Hawaiian humpback whales and conspecifics nearby. *Behav Ecol Sociobiol* 8:105–116
- Tyack, P. L., Sayigh, L. S. (1997). Vocal learning in cetaceans. In C. Snowdon, M. Hausberger (Eds.), *Social influences on vocal development*. Cambridge: Cambridge University Press, pp 208–233
- Urick, R. J. (1983). *Principals of underwater sound*. New York: McGraw-Hill
- von der Emde, G., Menne, D. (1989). Discrimination of insect wingbeat-frequencies by the bat *Rhinolophus ferrumequinum*. *J Comp Physiol A* 167:423–430
- Walker, M. M., Kirschvink, J. L., Ahmed, G., Dizon, A. E. (1992). Evidence that fin whales respond to the geomagnetic field during migration. *J Exp Biol* 171:67–78
- Watkins, W. A., Daher, M. A., Fristrup, K. M., Howald, T. J., di Sciara, G. N. (1993). Sperm whales tagged with transponders and tracked underwater by sonar. *Marine Mammal Science* 9:55–67
- Watkins, W. A., Schevill, W. E. (1979). Aerial observations of feeding behavior in four baleen whales: *Eubalaena glacialis*, *Balaenoptera borealis*, *Megaptera novaeangliae*, and *Balaenoptera physalus*. *J Mammal* 60:155–163
- Watkins, W. A., Schevill, W. E., Best, P. B. (1977). Underwater sounds of *Cephalorhynchus heavisidii* (Mammalia: Cetacea). *J Mammal* 58:316–320
- Watkins, W. A., Tyack, P., Moore, K. E., Bird, J. E. (1987). The 20-Hz signals of finback whales (*Balaenoptera physalus*). *J Acoust Soc Am* 82:1901–1912
- Watkins, W. A., Wartzok, D. (1985). Sensory biophysics of marine mammals. *Marine Mammal Science* 1:219–260
- Weilgart, L., Whitehead, H. (1988). Distinctive vocalizations from mature male sperm whales. *Can J Zool* 66:1931–1937
- West, M. J., King, A. P. (1988). Female visual displays affect the development of male song in the cowbird. *Nature* 334:244–246
- West, M. J., King, A. P. (1990). Mozart's starling. *Am Sci* 78:106–114
- Weston, D. E. (1967). Sound propagation in the presence of bladder fish. In V. M. Albers (Ed.), *Underwater acoustics*. New York: Plenum, vol 2
- Williams, H., Nottebohm, F. (1985). Auditory responses on avian vocal motor neurons: a motor theory for song perception in birds. *Science* 229:279–282
- Winter, P., Handley, P., Ploog, D., Schott, D. (1973). Ontogeny of squirrel monkey calls under normal conditions and under acoustic isolation. *Behaviour* 47:230–239
- Wrangham, R. W., Gittleman, J. L., Chapman, C. A. (1993). Constraints on group size in primates and carnivores: population density and day-range as assays of exploitation competition. *Behav Ecol Sociobiol* 32:199–209
- Würsig, B., Clark, C. W. (1993). Behavior. In J. J. Burns, J. J. Montague, C. J. Cowles (Eds.), *The bowhead whale*. Lawrence, KS: The Society for Marine Mammalogy
- Würsig, B., Würsig, M. (1979). Behavior and ecology of the dusky dolphin, *Lagenorhynchus obscurus*, in the south Atlantic. *Fish Bull* 77:871–890
- Xitco, M. J., Jr., Roitblat, H. L. (1996). Object recognition through eavesdropping: passive echolocation in bottlenose dolphins. *Animal Learning & Behavior* 24:355–365