

## Pinniped Sensory Systems and the Echolocation Issue

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Ronald J. Schusterman, David Kastak, David H. Levenson,  
Colleen Reichmuth Kastak, and Brandon L. Southall

### Introduction

Each species lives in its own sensory world, or *Umwelt*. Therefore, it is surprising that even though pinnipeds inhabit dark or murky water, as do odontocete cetaceans, pinnipeds apparently have not evolved sonar. Unlike odontocete cetaceans, pinnipeds do not seem to use echolocation to obtain prey, orient themselves with regard to relocating breathing holes after lengthy underwater excursions, or navigate at sea. While dolphins produce high-frequency clicks using specialized structures, exquisitely differentiate frequencies at the high end of their auditory range, and demonstrate very acute directional hearing and temporal resolution, comparable underwater abilities in pinnipeds are mundane at best. We suggest that most pinnipeds have not evolved echolocation because, unlike dolphins that are completely aquatic, pinnipeds are truly amphibious. Presumably, there has been little selective pressure on pinnipeds to evolve echolocation. Instead, they appear well adapted to combine and synthesize a variety of sensory cues, along with spatial memory to orient under water. The preponderance of evidence shows that pinnipeds use passive cues such as light, sound, and hydrodynamic and tactile stimuli to forage, avoid predators, and navigate.

At the first Animal Sonar Systems Symposium in 1966, significant issues were raised regarding the possibility that pinnipeds (seals, sea lions, and walruses) could echolocate. This proposition followed logically from the fact that echolocation had recently been demonstrated in the odontocete cetaceans (toothed whales and dolphins), which, like pinnipeds, must forage and navigate at times in dark and murky waters. At the symposium, two papers were presented that purported to evaluate the ability of California sea lions (*Zalophus californianus*) to echolocate. These papers caused quite a stir at the symposium, first because their results were in complete contradiction, and, ironically, because both scientists came not only from the same institution (the Stanford Research Institute) but also from the same laboratory (the Diving Mammals and Biosonar Lab). Despite some evidence to the contrary (Evans and Hagen 1963), Thomas Poulter believed that he had al-

ready demonstrated sophisticated echolocation abilities in California sea lions and suggested that other pinniped species also had developed specialized sonar abilities (Poulter 1963, 1967). However, Poulter's colleague, Ronald Schusterman, presented an opposing view. Schusterman concluded that his data, collected under highly controlled conditions, demonstrated that California sea lions did not use echolocation and instead relied on other sensory modalities, particularly vision, to navigate and forage under water (Schusterman 1967).

More than three decades later, due to the lack of any convincing supporting evidence, the pinniped echolocation hypothesis remains unproven within the field of marine mammal acoustics and behavior. Since the first Animal Sonar meeting, the idea that pinnipeds use echolocation has been periodically revived (Renouf and Davis 1982; Thomas et al. 1983) and refuted (Oliver 1978; Scronce and Ridgway 1980; Wartzok, Schusterman, and Gailey-Phipps 1984). In this volume, Evans et al. (chapter 71) and Awbrey et al. (chapter 70) revisit the pinniped echolocation hypothesis in light of new recordings of Weddell seals (*Leptonychotes weddelli*) navigating under the ice, and on the basis of expanded and updated descriptions of earlier observations (Thomas et al. 1983) of a single captive leopard seal (*Hydrurga leponyx*) that emitted high-frequency signals while chasing fish under relatively darkened conditions. These authors suggest that Antarctic pinnipeds, which inhabit ice-covered areas and live in relative darkness during part of the year, are the most likely pinniped species to have evolved a specialized echolocation system for use in foraging and navigation.

The aim of this chapter is to review the echolocation hypothesis in the context of our current understanding of pinniped sensory systems. We find it necessary to first make a clear distinction between echolocation in a general sense and echolocation as a specialized ability. For instance, there is some experimental evidence that blind and sighted humans can be trained to detect, locate, and discriminate targets by listening for reflected echoes (Rice, Feinstein, and Schusterman 1965). Blinded rats, on the other hand, are capable of opportunistically using echoes of the sounds generated by their own movements to find their way through a maze (Riley and Rosenzweig

1957). While neither humans nor rats have evolved specialized echolocation abilities, these performances have been shown to emerge through experience.

In the following pages, we consider the issue of whether some pinniped species possess specialized sound production, detection, and signal-processing abilities for underwater echolocation similar to the type shown by odontocete cetaceans. We will argue that unlike the aquatic dolphins, pinnipeds have not developed active biosonar; rather, the amphibious lifestyle of pinnipeds has resulted in relatively nonspecialized underwater hearing abilities. Instead of using active biosonar, pinniped species appear to depend on alternative sensory capabilities—such as underwater hearing (passive biosonar), enhanced vision, and acute hydrodynamic reception—to orient in the marine environment. We address the issue of echolocation in pinnipeds by discussing sound production mechanisms and amphibious hearing capabilities, each in comparison to similar capabilities in odontocetes. Finally, we explore, from an experimental and ecological point of view, the use of the supplementary senses of vision and tactile/hydrodynamic sensitivity by pinnipeds to forage and navigate underwater.

### Sound Production

In addition to social vocalizations, bottlenose dolphins (*Tursiops truncatus*) produce broadband echolocation clicks with significant energy at frequencies above 90 kHz (see Au 1993 for a comprehensive review of cetacean echolocation performance). The clicks are extremely loud (218–228 dB re 1  $\mu$ Pa), probably to compensate for transmission losses associated with spreading and absorption in water. Dolphins possess specialized sound production and transmitting structures not found in other mammals—sound is transmitted from the forehead and received primarily through acoustically sensitive areas of the lower jaw. Dolphins also appear to exercise fine control over the beam pattern and spectral and temporal content of their short (50–70  $\mu$ s per pulse) echolocation click trains. The acoustic properties of the signal directly relate to environmental variables such as target range and ambient noise.

Pinnipeds also produce a wide variety of signals underwater, including whines, grunts, roars, chirps, trills, chugs, and pulsed sounds (reviewed by Richardson et al. 1995). Many of these sounds are known to be related to social behavior and reproduction; however, the emission of high-frequency and pulsed sounds by a few species has led some researchers to speculate about the existence of echolocation in pinnipeds. Because pinnipeds produce underwater sounds, it is worthwhile to ask whether these sounds could function in a manner analogous to the echolocation pulses produced by odontocetes. The features of pinniped underwater sounds that make them appeal-

ing as potential echolocation signals are those that resemble dolphin biosonar sounds. Many pinniped sounds are pulsatile and repetitive, and at least one captive recording contained ultrasonic components (Awbrey et al., chapter 70, this volume). Further, some of these sounds have been recorded in nonsocial contexts, such as foraging or spatial orientation (Evans et al., chapter 71, this volume).

However, the sounds produced by pinnipeds differ from those produced by dolphins in some important ways. First, source levels are relatively low, ranging from only about 90–190 dB (re 1  $\mu$ Pa) (see Richardson et al. 1995). Second, some of these sounds—for example, FM sweeps—are long in duration and emitted almost continuously. It is unlikely that this pattern of sound production allows for detection of echo returns between outgoing signals. Further, the relatively long durations of the calls increase the likelihood of contamination from reverberation, an important consideration for under-ice echolocation. Even the shorter-duration pulses produced by pinnipeds (0.3 to >10 ms) are much longer than those produced by dolphins. While potentially useful in the detection of large objects, the pulse durations typical of pinnipeds would not allow the fine target resolution seen in odontocetes. Third, in contrast to the dolphins, pinnipeds do not appear to modify the temporal patterning of click signals according to target range in laboratory tests of echolocation performance (Schusterman 1967); however, field observations of Weddell seals suggest that pulse rates increase as the seals approach ice holes (Evans et al., chapter 71, this volume). Fourth, the underwater sound detection capabilities of pinnipeds are inferior by about 20 dB at best sensitivity to those of dolphins. Finally, pinnipeds are less adept at localizing sound and detecting very brief stimuli than are the odontocetes (see Richardson et al. 1995). As a result of all of these factors, it is unlikely that the pinnipeds are consistently producing sounds with sufficient intensity to provide much environmental information by way of echo returns. All of these observations suggest an auditory/acoustic channel that is qualitatively different from that present in odontocete cetaceans, in terms of sound production, sound reception, and orienting behavior.

Attention has recently focused on the Antarctic leopard and Weddell seals, which are known to be extremely vocal underwater and to forage under conditions of near darkness. These factors have led some researchers to consider the possibility of echolocation in these species (Awbrey et al., chapter 70, this volume; Evans et al., chapter 71, this volume). However, underwater observations of foraging Weddell seals made by Davis et al. (1999) contradict echolocation-based explanations of foraging. These investigators found that seals fitted with portable video cameras did not emit vocalizations while pursuing prey. Rather, the seals appeared to use vision to detect

and track the movements of fish. Given the generally low frequencies and source levels of Weddell seal calls, as well as the weak target strengths of typical prey items, it is unlikely that this species is able to detect prey using active biosonar. Additionally, speculation of under-ice navigation by Weddell seals via biosonar is not supported by the results of another recent study, which indicated that only half of the seals surfacing in ice holes produced any sounds at all (Evans et al., chapter 71, this volume).

What, then, are the functions of the underwater sounds produced by pinnipeds, if not for echolocation? The answers likely lie in social behavior. Phocids (true seals), which produce underwater sounds most frequently, generally breed in water, and their underwater vocalizations are almost certainly related to breeding behavior. In otariids (sea lions and fur seals), variability in signal strength, repetition rate, and other vocal parameters often is related to affect or motivational state. This observation explains the underwater sounds produced by subjects in a state of arousal while chasing fish in a tank (Schusterman 1967). The specific functions of underwater vocalizations are likely to be further elucidated when more data on the underwater behavior of these animals becomes available. Based on our current limited understanding of certain species, it remains possible that some pinnipeds are capable of specialized echolocation. However, given the extreme paucity of evidence after more than thirty years of investigation, to say that it is unlikely would be an understatement, especially when this ability has been so easily demonstrated in the odontocetes.

### Pinniped Auditory Sensitivity

When examining the pinniped auditory system, it is helpful to adopt a phylogenetic perspective—all pinnipeds are carnivores, and their closest relatives are semiaquatic or terrestrial. Apart from a few anatomical modifications, the pinnipeds retain the basic, air-adapted carnivore ear, even after more than 25 million years of divergence from a common ancestor (Repenning 1976). Thus, it is likely that the pinniped auditory system functions in much the same way as that of most terrestrial mammals. In contrast, the odontocete ear has become extremely modified from its original air-adapted form and bears little resemblance to any sort of terrestrial mammalian ear. When the results of behavioral experiments on aerial and underwater hearing sensitivity in pinnipeds are expressed in terms of the detection of sound energy, they clearly support the proposition that the pinniped ear is adapted to hear in water rather than in air. However, when the metric of comparison is changed to sound pressure, a different picture emerges—the otariids are adapted to hear in air, while the phocids are generally adapted for amphibious hearing (Kastak and Schusterman 1998). The northern elephant seal

(*Mirounga angustirostris*), a deep diving phocid, shows differences in aerial and underwater sensitivity paralleling those of the bottlenose dolphin, implying aquatic specialization (Kastak and Schusterman 1998). When pairwise comparisons are made of air-water sensitivity between all pinnipeds tested to date in air and water, significant differences emerge only between phocids and otariids, and between the elephant seal and all other pinnipeds. The patterns of air and water hearing sensitivity appear to correspond to the patterns of life history of three pinniped assemblages: the otariids, the generalized phocids (*Phoca* spp.), and the northern elephant seal, a specialized phocid (Kastak and Schusterman 1998, 1999). Contrary to earlier interpretations of air-water sensitivity differences, which labeled the pinniped ear as “water-adapted,” the logical conclusion based on this reinterpretation is that all pinnipeds have retained some degree of airborne hearing sensitivity while developing enhanced underwater hearing. Retention of airborne sensitivity constrained the development of the exceptional underwater auditory sensitivity necessary for echolocation. In other words, the pinniped ear has evolved through natural selection to function amphibiously, perhaps at the cost of evolving an active biosonar system.

### Passive Biosonar

Laboratory experiments showing that pinnipeds can locate prey items rapidly under darkened conditions (Schusterman 1967), and reports of free-ranging, apparently blind pinnipeds surviving for long periods of time (Schusterman 1981), suggest that visually impaired seals and sea lions are able to find and capture prey, as well as orient in water and on land. Thus, one or more sensory mechanisms other than vision can apparently be used by pinnipeds when vision is of limited use. As previously discussed, the underwater hearing abilities of pinnipeds are not as acute as those of odontocetes. However, at low and intermediate frequencies, the underwater hearing sensitivity and sound localizing capabilities of pinnipeds (reviewed in Richardson et al. 1995) suggest that simply by listening, they may obtain information regarding the presence and general location of prey, predators, conspecifics, and navigational landmarks.

The practical functions of underwater hearing in free-ranging pinnipeds remain largely uninvestigated. However, experiments in the field by Wartzok et al. (1992a) showed that blindfolded ringed seals (*Phoca hispida*) and Weddell seals used experimentally produced acoustic cues to find novel holes cut through the ice. When these acoustic cues were removed, the blindfolded seals were able to return to the same ice holes, presumably using spatial memory or ambient noises rather than active biosonar, evidenced by the fact that they did not produce sounds while searching for ice holes.

Given that many pinnipeds hear well in water, what underwater sounds are of biological relevance to them? At least one experiment suggests that predator detection is an essential function of underwater hearing. Schusterman and Kastak (1996) found that a northern elephant seal, in contrast to a California sea lion and a harbor seal (*Phoca vitulina*), exhibited an exaggerated startle response and quickly became sensitized to pulsatile sounds resembling the echolocation clicks of killer whales. These observations, in addition to reports that mammal-hunting killer whales echolocate less frequently and in a more unpredictable fashion than those that hunt fish (Barrett-Lennard, Ford, and Heise 1996), indicate that predator detection is accomplished, at least in part, simply by listening.

### Vision

One of the most striking features of pinniped anatomy is the large size of the eyes. Early in the study of pinniped sensory systems, it was realized that the enhanced light-gathering ability of an enlarged eye was of tremendous advantage for visual foraging in a relatively dark environment. Studies on anatomy and photorefractive properties have shown that the eyes of these amphibious mammals are suited primarily for vision in water rather than in air, possessing large, round lenses to compensate for the absence of corneal refraction under water (Johnson 1893; Walls 1942). The pupil of pinnipeds is stenopaic (slit-like) and probably functions as a pinhole aperture, providing relatively clear vision in air, as long as the pupil remains small (Walls 1942). Behavioral studies confirmed the pupil's role in aerial visual acuity when it was demonstrated that acuity drops off much faster in air than under water as ambient light levels decrease (Schusterman and Balliet 1971).

Like other mammals adapted for vision in dim conditions, pinnipeds possess large lenses and pupils, and densely packed, rod-dominated retinas with well-developed choroidal tapeta (Walls 1942; Landau and Dawson 1970). In circumstances where light levels change dramatically in a short period of time, it is advantageous to possess a pupil with a large dynamic range. This allows for efficient regulation of the illumination of retinas, functioning only secondarily to improve visual resolution. Substantial differences in pupillary dynamic range between shallow and deep-diving pinnipeds have been observed (Levenson and Schusterman 1997), illustrating the importance of the pupillo-motor response in maintaining sufficient photoreceptor stimulation. The deepest-diving pinniped, the northern elephant seal, exhibited a greater than 400-fold increase in pupillary area, while shallow and moderately deep divers demonstrated considerably smaller ranges of only 25- to 200-fold (Levenson and Schusterman 1997). The functional significance of differences in pupillary struc-

ture was clearly shown in a comparison of the dark adaptation rates of pinnipeds (Levenson and Schusterman 1999). The time necessary to reach maximum sensitivity was substantially faster for the elephant seal than for the shallower diving California sea lion and harbor seal. From an ecological standpoint, the six-minute dark adaptation time of the elephant seal (Levenson and Schusterman 1999) matches the time it takes these seals to dive from the surface to foraging depths of 300–700 m (LeBoeuf and Laws 1994).

The elephant seal is as extreme in terms of adaptation for underwater vision as it is for underwater hearing. In addition to having an extremely rapid dark adaptation rate, the eye of the elephant seal is very light sensitive and possesses specialized rod photopigments. Consequently, the elephant seal visual system is designed not only to respond rapidly to changes in light level, but to take advantage of very low levels of the shorter wavelengths of light that predominate deep under water (Lythgoe and Dartnall 1970). The shallower diving harbor seals and California sea lions are less light sensitive than the elephant seal, and they possess rod pigments with sensitivity only slightly shifted to short wavelengths compared to those of terrestrial mammals (Lavigne and Ronald 1975; Jacobs et al. 1993; Levenson and Schusterman 1999).

Pinniped visual systems, though amphibious, are primarily water adapted. As suggested by earlier studies (reviewed in Schusterman 1981), underwater foraging and navigation likely depend to a great extent on the ability to see well in this medium. Natural selection in these animals clearly has favored the development of visual systems suited to foraging and navigation in an aquatic environment.

### Tactile/Hydrodynamic Sensitivity

While benthic feeding dolphins have been observed to direct echolocation pulses into the substrate to detect prey (Rossbach and Herzing 1997), pinnipeds such as walrus that forage on the muddy sea floor tend to have modified vibrissae and facial structures to detect and extract prey from the bottom (Riedman 1990). Even pinnipeds that forage on swimming prey have vibrissae that are highly specialized with respect to size, length, vascularization, and innervation. These structures are apparently used to detect tactile and hydrodynamic cues very close to the source, and thus the tactile sense has been implicated in foraging (Davis et al. 1999) and very short-range navigation (see Riedman 1990).

Because pinniped vibrissae are exquisitely sensitive to vibration, it is possible that they function in detecting particle motion associated with the flow field of a moving fish or the acoustic near field of struggling prey (Dehnhardt, Mauck, and Bleckmann 1998). This ability would be especially useful in the final stages of prey pur-

suit, when vision would be of questionable use because the visual field is directed forward, above the head, and away from the mouth. One can envision the sensory systems used during prey detection, pursuit, and capture by pinnipeds as follows: The prey is detected visually (preferentially backlit against the surface water or ice) or acoustically (by eavesdropping on intraspecific signals produced by the fish or incidental sounds produced by swimming). Pursuit is guided visually and perhaps acoustically, and fine-scale orientation on the prey is mediated by detection of the flow field around the fish by the vibrissae, leading to prey capture.

### Conclusions

Odontocete cetaceans possess a highly sophisticated system of active biosonar. This system involves the production of high-intensity, high-frequency clicks in a directional beam. Received echoes can provide information about target location and identity, and typical targets can be detected accurately at distances of over 100 m (Au 1993). Echolocation in this group is tied to the development of sophisticated sound production, reception, and signal-processing systems, including excellent high-frequency sensitivity, highly directional hearing, and acute temporal and frequency resolution (Au 1993). This type of echolocation system evolved only once in the marine environment, in a group of organisms that became completely tied to an aquatic existence. Because odontocetes were not evolutionarily constrained to give birth on land, the dolphin auditory system became fully adapted for underwater functioning, allowing a refinement of the biosonar system not possible in am-

phibious mammals, such as the pinnipeds. Because even the most aquatic pinnipeds must return to shore periodically and because airborne vocal communication appears to play an important role in most, if not all, pinniped social systems, selection pressures for highly sensitive, acute underwater hearing have not shaped the pinniped auditory system to as great an extent as in dolphins. Rather, the retention of in-air hearing abilities has limited the sensitivity of hearing under water, where all pinnipeds must forage. Consequently, instead of developing a primarily sound-based system of underwater orientation, pinniped visual, tactile, hydrodynamic, and acoustic sensory systems were refined and incorporated into overlapping underwater perceptual channels that permit efficient underwater foraging and navigation without the use of active biosonar.

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### Ultrasonic Underwater Sounds from a Captive Leopard Seal (*Hydrurga leptonyx*)

Frank T. Awbrey, Jeanette A. Thomas, and William E. Evans

#### Introduction

The leopard seal (*Hydrurga leptonyx*) is a large Antarctic pack-ice phocid that feeds predominantly on krill, fish, and cephalopods, but also is known to prey on seal pups and penguins during the austral summer. In this solitary species, males and females are seen together

only during a brief mating period in November (Siniff 1991). The underwater sound repertoire of leopard seals has been studied in the wild by Stirling and Siniff (1979), Thomas and DeMaster (1982), Rogers, Cato, and Bryden (1995), and Thomas and Golladay (1995) using audio recording equipment. These investigators reported 5–12 underwater sound types, depending on the location