

Low-frequency amphibious hearing in pinnipeds: Methods, measurements, noise, and ecology

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Aerial low-frequency (100–6400 Hz) hearing thresholds were obtained for one California sea lion (*Zalophus californianus*), one harbor seal (*Phoca vitulina*), and one northern elephant seal (*Mirounga angustirostris*). Underwater thresholds over a similar frequency range (75–6300 or 6400 Hz) were obtained for these three animals in addition to another California sea lion. Such data are critical, not only for understanding mechanisms about amphibious hearing and relating them to pinniped ecology and evolution, but also for identifying species at risk to man-made noise in the marine environment. Under water, the elephant seal was most sensitive, followed by the harbor seal and the sea lions. In air, the harbor seal was most sensitive, followed by the older of the two sea lions and the elephant seal. The following trends emerged from comparisons of each subject's aerial and underwater thresholds: (a) the sea lion (although possessing some aquatic modifications) is adapted to hear best in air; (b) the harbor seal hears almost equally well in air and under water; and (c) the elephant seal's auditory system is adapted for underwater functioning at the expense of aerial hearing sensitivity. These differences became evident only when aerial and underwater thresholds were compared with respect to sound pressure rather than intensity. When such biologically relevant comparisons are made, differences in auditory sensitivity can be shown to relate directly to ecology and life history. © 1998 Acoustical Society of America. [S0001-4966(98)01804-9]

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INTRODUCTION

Richardson *et al.* (1995) outlined the current state of knowledge with respect to the hearing abilities of marine mammals. These authors noted a distinct lack of data on low-frequency hearing, specifically frequencies below 1000 Hz. These data are crucial, considering recent concerns about anthropogenic noise in general, and specifically, low-frequency sound produced by oil drilling, seismic exploration, shipping, and oceanographic experiments. There are little available data on the low-frequency hearing abilities of pinnipeds, including the Phocidae (true seals) and Otariidae (sea lions and fur seals). The northern elephant seal is a species of particular concern because of its geographic range (proximity to shipping lanes as well as ATOC transmission paths) and its deep-diving ability. This study examines the low-frequency (below 6400 Hz) hearing of three species of pinniped, the harbor seal (*Phoca vitulina*), the California sea lion (*Zalophus californianus*), and the northern elephant seal (*Mirounga angustirostris*) using behavioral psychophysics. The absolute auditory thresholds obtained are placed in a comparative framework which relates hearing sensitivity to components of pinniped biology. These factors are divided into several categories: pinniped vocal behavior; auditory anatomy; amphibious hearing, including a consideration of the "adequate" acoustic stimulus with respect to sound source specification; the relationship between low-frequency hearing and the effects of noise; and finally, evolutionary and ecological considerations.

A. Pinniped vocal behavior and hearing

Airborne vocalizations by pinnipeds play important roles in social functions, including the delineation of terri-

tory, advertisements of dominance status, and female attendance behavior [for example, see Bartholomew and Collias (1962); Peterson and Bartholomew (1969); Schusterman *et al.* (1992)]. Some underwater vocalizations are also related to social interactions, particularly among breeding males [see Schusterman (1978) for review]. However, despite the initial claim by Poulter (1963) and later revived by Renouf and Davis (1982), that many pinniped sounds were biological sonar signals, experimental evidence for such claims has come under heavy criticism (Evans and Haugen, 1963; Schusterman, 1967; Schusterman, 1981; Wartzok *et al.*, 1984). In general, phocids are far more vocal under water than are otariids, although evidence for underwater sound production in elephant seals and monk seals is sparse [for a review, see Watkins and Wartzok (1985)].

Descriptions of the aerial and underwater sound production by pinnipeds suggest that these animals ought to possess amphibious hearing, and indeed, available evidence confirms this hypothesis. The hearing sensitivity of the ringed seal (Terhune and Ronald, 1975), harp seal (Terhune and Ronald, 1971, 1972), harbor seal (Möhl, 1968a; Turnbull and Terhune, 1990; Terhune, 1991), California sea lion (Schusterman *et al.*, 1972; Schusterman, 1974), and northern fur seal (Moore and Schusterman, 1987; Babushina *et al.*, 1991) have been behaviorally measured at frequencies above 1 kHz. Sensitivity to underwater sounds has generally been reported to be as good as or better than sensitivity to aerial sounds in all these species. The superiority of underwater sensitivity was first noted by Möhl (1968a) and later corroborated by Moore and Schusterman (1987), Terhune (1989) and Babushina *et al.* (1991).

Pinnipeds evolved from terrestrial carnivores, whose

outer and middle ears are adapted to hear airborne sound. Such an ear should be ineffective under water because of the impedance mismatch between air and water and therefore the ability of a pinniped to hear well under water is intriguing (Repenning, 1972). The 30 or so dB hearing loss in submerged humans (Wainwright, 1958) is thought to occur because under water, the sound transmission path to the inner ear shifts from middle ear conduction to bone conduction through the skull (Hollien and Brandt, 1969). Repenning (1972) hypothesized that bone conduction also occurs under water in the pinnipeds, but is enhanced relative to humans by modifications in the bones of the skull. However, he and others (Møhl, 1968b; Ramprasad, 1975; Moore and Schusterman, 1987; Terhune, 1989) also suggested that changes in the middle ear that occur upon submersion may allow it to function in a conventional fashion during diving; that is, to transmit acoustic energy to the inner ear via the tympanic route. The role of the middle ear as a variable transformer (i.e., similarity of function in air and under water accomplished by impedance matching to both media) received some experimental support from Møhl and Ronald (1975) who measured the cochlear microphonic response of a harp seal and determined that under water, sound was most efficiently transmitted to the inner ear along the external meatus. The results suggest that acoustic energy may be preferentially channeled through the lumen, walls, and/or surrounding tissue of the ear canal when the seal is under water. Additional data from the same animal suggest that the effective interaural distance corresponds to the separation of the external auditory meatal openings, and not the interbullar distance, which would be expected if massive bone conduction was the predominant mode of hearing (Møhl and Ronald, 1975). This suggests that pinnipeds are likely to rely upon "conventional" sound conduction pathways as well as bone conduction to detect underwater acoustic signals (see, e.g., Ramprasad, 1975).

B. Underwater functioning of the pinniped ear

The gross anatomical characteristics of the pinniped ear are suggestive of adaptation for aerial hearing, but some features are presumed to enable rather efficient underwater hearing (King, 1983). Detailed anatomical observations of the pinniped ear can be found in Repenning (1972) and Ramprasad *et al.* (1972). There are several notable differences between the two major pinniped families.

Phocids lack an external ear pinna. The external meatus is long, narrow, and filled with cerumen and hairs. It is supported by cartilage throughout most of its length, and is flexible and easily collapsed. Muscular attachments allow closure of the meatal opening, although it is unclear whether the canal is air-filled under water. The middle ear bones are larger and more dense than those of terrestrial mammals. These bones are loosely attached to the inner wall of the middle ear, and surrounded by a highly vascularized corpus cavernosum or cavernous tissue (Møhl, 1967, 1968b; Ramprasad, 1975), which is also found in the external meatus. The round window is partly or entirely shielded from the middle ear space in both the phocids and the otariids. In the elephant seal, the round window opens at the junction of the

bullae and the mastoid, to the exterior of the skull (Repenning, 1972). In contrast to the phocid ear, the ear of otariids has a pinna, which is greatly reduced when compared to the pinnae of terrestrial carnivores and is often considered vestigial. The middle ear bones of otariids are less massive than those of phocids, but cavernous tissue is present and highly developed in both the meatus and middle ear space (Odend'hal and Poulter, 1966).

Møhl (1968b), as well as Odend'hal and Poulter (1966), Repenning (1972), and later Moore and Schusterman (1987) and Terhune (1989) suggested that the pinniped middle ear might function as a variable transformer, allowing these animals to hear well in air and with better than expected sensitivity in water. According to this hypothesis, as a pinniped dives, the cavernous tissue of the middle ear and external meatus engorges with blood. This may be an active mechanism, accompanying changes in blood circulation that take place during the dive response (Castellini *et al.*, 1994), or a passive response to pressure changes at depth. The swelling of cavernous tissue collapses the lumen of the external meatus as well as the middle ear air space, increasing its acoustic impedance to more closely match that of the surrounding water. This impedance change ostensibly reduces the reflection of sound energy from the tympanic membrane. Under extreme pressures, both sides of the tympanic membrane will contact fluid (tissue in the meatus and in the middle ear), allowing sound to be transmitted efficiently to the cochlea through the ossicular chain because of the minimized impedance difference across the tympanic membrane. Such hearing in the "conventional" sense ought to occur at depths below about 80–100 m (Repenning, 1972), because at these depths pressure-induced volume changes in the middle ear should cause cavernous tissue to contact both sides of the tympanic membrane.

C. Pressure versus intensity

It has become standard practice, when comparing aerial and underwater hearing, to convert sound pressure into sound intensity, correcting for the impedance difference between air and water [see Carey (1995) for a discussion of suggested reference units for underwater sound]. This practice has been justified on the presumption that underwater hearing takes place via bone conduction, rather than "conventional" pressure transduction. Sound energy reaching the inner ear in this fashion is often assumed to be transferred via particle displacement, or one of its derivatives, velocity or acceleration (Lombard and Hetherington, 1993). While both the inner ear and lateral line systems of many fish are sensitive to acoustic particle motion rather than pressure (Harris and van Bergeik, 1962; Kalmijn, 1989), many aquatic or amphibious animals, such as otophysine fish (Popper and Fay, 1973, 1993) and certain frogs (Hetherington and Lombard, 1982) have been shown to be sensitive to sound pressure rather than, or in addition to, particle motion. These animals make use of functional analogs to the mammalian middle ear to detect pressure fluctuations related to acoustic phenomena. It is reasonable to suggest that the pinniped ear responds to acoustic pressure (rather than particle motion) when submerged, since it possesses the typical mammalian

middle ear structures. However, partly because of a lack of understanding of the “adequate stimulus” for underwater hearing in mammals, and partly because of recent interdisciplinary crossing-over among biologists and ocean engineers, measures of intensity have been adopted as a means of comparing aerial and underwater sound, and consequently, hearing thresholds in amphibious animals.

Intensity is strictly a measure of the rate of energy flow in the sound field. Therefore it can be used as a basis of comparison without considering the transduction of sound energy from the environment to the receiver’s auditory system. In addition, its use is already accepted by ocean engineers and acousticians (Carey, 1995). The use of intensity is problematic, however, since it is not directly measured but rather estimated from pressure measurements using the equation $I = p^2 / \rho c$. This equation describes the relationship between pressure and intensity in a plane progressive wave, free from boundaries and reflection. In practice this relationship rarely holds, especially in test tanks (mainly due to the presence of reflective boundaries), where intensity can be underestimated, sometimes by one or more orders of magnitude (Lombard *et al.*, 1981). Further, it is extremely difficult to directly measure intensity under these conditions, especially when the acoustic stimuli consist of pure tones (Fahy, 1989). Test environments which are far from ideal in these terms include shallow tanks, ocean pens in shallow water, and the hydrodynamic near field of a projector. All data published on underwater hearing in marine mammals were obtained under at least one of these three conditions. Although sound-pressure thresholds obtained in such studies are accurate, intensity calculations based solely on these pressure thresholds are likely to be in error.

In this experiment, our approach was to compare aerial and underwater thresholds with respect to pressure (in addition to intensity) for three reasons: (1) the difficulties in estimating intensity in our testing situation precluded the determination of accurate intensity thresholds; (2) there is a body of data (see discussion) implicating pressure as the primary stimulus to which the pinniped ear is sensitive under water; and (3) comparisons using pressure rather than intensity illustrate the relative amphibious adaptations of the three species we tested, because the pinniped ear appears to have retained its pressure transducing capabilities in air (Möhl, 1968b; Repenning, 1972; Ramprasad, 1975).

D. Man-made noise

Even though we know that some species of pinnipeds are quite sensitive to frequencies ranging from 1 to about 50 kHz, virtually nothing is known about their low-frequency hearing sensitivity. Since most man-made sounds are low in frequency, and the levels of such noise in the ocean are increasing (Urick, 1986), the impact of anthropogenic sound in the ocean on pinnipeds is largely unknown. In a band between about 20 and 200 Hz, ambient noise in the ocean is dominated by shipping noise. This noise is higher in shipping lanes, along coasts, and in bays and harbors; however, sounds can propagate great distances with little loss, depending on oceanographic conditions (see Urick, 1983; Richard-

son *et al.*, 1995, for reviews). Other sources of anthropogenic noise in the ocean are sounds from construction, ice-breaking, oceanographic experiments, and oil drilling operations. All of these sounds have the potential to interfere with acoustic signal detection in aquatic animals, but only if (1) the animals are sensitive to sounds similar in frequency, and/or (2) the sounds are loud enough to mask biologically relevant acoustic signals or to cause temporary or permanent damage to the auditory system. In light of recent increases in anthropogenic noise and concerns about acoustic habitat degradation, low-frequency hearing thresholds for a variety of species should be considered critical data.

The goals of the experiments described in this paper are to characterize the low-frequency aerial and underwater hearing sensitivity of individual animals representing three pinniped species, two relatively shallow divers (*Zalophus* and *Phoca*) and one deep diver (*Mirounga*). The procedures utilize operant conditioning of behavioral responses to pure tones to determine auditory thresholds (Stebbins, 1970). The resulting data are compared with respect to medium (air or water) and species and related to ecology, evolution, life history, and auditory anatomy.

I. METHODS

A. Acoustic mapping

The acoustic response of a 7.6-m test pool to low-frequency pure tones was mapped prior to the audiometric tests on three pinnipeds. Pure tones at frequencies ranging from 100 to 1000 Hz were projected from a J9 underwater transducer. Measurement was made with an H56 calibrated hydrophone, a Tektronix oscilloscope, and a General Radio Company type 1554A vibration and noise analyzer equipped with third-octave filters to measure ambient noise. Once a region of sufficient and constant signal intensity was located, its position was recorded. Away from its walls, the tank had good response i.e., a signal with minimal fluctuations in amplitude was measured) to all frequencies below 1 kHz with variable reliability (some amplitude variation) at frequencies between 1600 and 6400 Hz. Although higher-frequency signals could be produced and received, frequency-dependent amplitude fluctuations of up to 10 dB were apparent. Reliability at frequencies much higher than 6400 Hz was generally poor. Once an area of maximal intensity was mapped, the experimental apparatus was arranged so that the subjects could be trained to station in that position for threshold testing.

B. Subjects

The subjects of aerial threshold testing were Rocky, a female California sea lion (*Zalophus californianus*), aged 17–19 years during the course of the experiments, Sprouts, a male harbor seal (*Phoca vitulina*), aged 5–7 years during testing, and Burnyce, a female northern elephant seal (*Mirounga angustirostris*), aged 1–3 years during testing. These three animals, in addition to Rio, a female *Zalophus* aged 7–9 years, were the subjects of the underwater hearing experiments. All three animals were kept in free-flow saltwater pools and adjacent haulout areas at Long Marine Laboratory

in Santa Cruz, California. They were fed a mixed diet of herring and capelin (4–10 kg per day), and usually consumed 20%–30% of a daily ration during test sessions.

Neither of the sea lions nor the harbor seal had ever been treated for disorders involving the ear. Although these subjects were occasionally treated with antibiotics, aminoglycosidic compounds were never used. The elephant seal, however, developed a chronic otitis externa prior to being tested. The infection was confined to the right external meatus, and occurred following an intrusive procedure conducted at Hubbs-Sea World Research Institute (Yochem, personal communication). The ear was treated both systemically and topically. Hair cell damage caused by topical administration of neomycin was determined to be extremely unlikely given the external localization of the infection. Aminoglycosidic compounds were not administered systemically.

C. Apparatus

1. Aerial

In-air threshold measurements were obtained outdoors, on a haulout space adjacent to the test pool. The aerial response apparatus was an approximately cubic PVC box measuring 45×45×63 cm. Two metal slots were attached to the inside front face of the apparatus. An opaque Plexiglas door (39×45 cm) was mounted in these slots and connected to a rope and pulley assembly. The door served to separate a chin station and a response paddle.

2. Underwater

The response apparatus was a larger version of the one used in air. The dimensions were 43×135×100 cm. The relative positions of projector and receiver were modified to maintain a uniform sound field at the chin station during all phases of testing.

D. Stimuli

1. Aerial

Pure tones were produced by a Stanford Research Systems DS345 function generator and SRS Arbitrary Waveform Composer software run on a 486-based PC. All waveforms were 500 ms in duration, and shaped with rise–fall times of 40 ms to eliminate switching transients. Waveforms were monitored on a Hitachi V202 oscilloscope. Signals were triggered manually from the function generator. The output of the DS345 was fed to an H-P 350C stepwise attenuator, then to a Realistic MPA-20 power amplifier. Signals were presented to the subjects through Telephonics TDH-39 earphones that were secured to pockets of specially designed neoprene harnesses. The earphone openings were placed directly over the ears of the subjects. Signal measurements at the opening of the external meatus were made with an Etymotic Research ER-7C clinical probe microphone system. Ambient noise levels under the earphones were determined in third-octave bands using the probe microphone, a PC sound card (22-kHz sampling rate, 16-bit recording) and Spectra Plus software (Pioneer Hill). At frequencies below 1 kHz, placement of the earphones decreased ambient noise at the meatus by approximately 7–15 dB.

2. Underwater

Pure tones for underwater testing were generated in the same manner as the in-air signals. All waveforms had durations of 500 ms and rise–fall times of 40 ms. The signals were projected by a J9 underwater transducer. The J9 was placed 135 cm away from the pool wall and 157 cm below the pool rim, on the horizontal axis shared by the stationing arm. The distance between the J9 and the end of the stationing arm was approximately 5 m. Sound-pressure levels were recorded at the stationing device by a calibrated H56 hydrophone. Signal waveforms were monitored for distortion on the V202 oscilloscope during all phases of testing the three animals. Additionally, the PC-based real-time spectrum analyzer was used to monitor signal and noise levels on a trial to trial basis.

E. Procedure

1. Aerial

Prior to the start of a session, the subject was called out from the pool and the headphones were fitted into position by a trainer. Before each trial, the placement of the headphones was checked and the subject was required to place its nose on the station. When the subject was stationed properly, a concealed assistant raised the door to expose the response paddle. The opening of the door served as a “ready” signal for the animal. The door remained open between 5 and 7 s. The experimenter observed the session on closed-circuit video, and could communicate with the trainer through a microphone attached to an in-air speaker. For a signal trial, the stimulus was triggered by the experimenter between 2 and 4 s after the door opened. The trainer had no knowledge of the presence or absence of a signal. A correct detection occurred if the animal pressed the paddle. If the trial was a catch trial (no signal), a correct rejection occurred if the animal remained stationed until the door was closed, signifying the end of the trial. All correct responses were confirmed by the experimenter and the information was relayed to the trainer. Subsequently, the trainer would reinforce the response with a piece of fish. Incorrect responses were not reinforced, and the animal was simply restationed following these trials.

2. Underwater

Prior to the start of each underwater trial, the subject was instructed to swim down to the station by a trainer seated at the side of the pool. After the subject was properly stationed, a trial began when an assistant opened the door to expose the response paddle. Trial durations were similar to those used in air (5–7 s). Reinforcement for correct responses was delivered by the trainer upon instruction by the experimenter; incorrect responses were not reinforced.

3. Psychophysical techniques

The experimental protocols for sessions and threshold determination were set up the same way for both aerial and underwater experiments. Signal and catch trials were presented quasirandomly, with a conditional probability of 0.50 for either trial type (Moore and Schusterman, 1987). A series

of two psychophysical methods was used to obtain thresholds. The first was a tracking or “staircase” method (Cornsweet, 1962), in which the signal intensity was decreased by 4 dB for each correct detection (hit). Following the first failure to detect a signal (miss), the increments were changed to 2 dB (increased for misses, decreased for correct detections). The sound level was not altered after catch trials. After three to five sessions in which consistent reversals occurred, a threshold was estimated as the average between the upper and lower limits of the reversals.

Following preliminary threshold estimation, a final threshold was obtained using a method of constant stimuli (Stebbins, 1970). A series of five or six sound levels (separated by 2 or 4 dB) was chosen from a 12–20-dB range surrounding the estimated threshold. Determinations of the number of signal levels and their separation were made following the staircase phase. These determinations were based on the range of variability in the subject’s staircase performance. Four or five trials of each signal level were arranged randomly within each session so that the subject could not respond on the basis of systematic changes in signal intensity. Sessions were composed of either 40 or 60 trials, depending on the number of stimulus levels used. As in the staircase sessions, 50 percent of the trials in each session were catch trials.

Threshold determination using the method of constants was based on Finney’s (1971) probit analysis. Most thresholds were determined using probit methods in the following fashion: a minimum of two sessions using the method of constants were run for each frequency. If, after two sessions, the 95% confidence limits of the threshold estimate fell within ± 3 dB, that estimate was used as the final threshold. If the confidence limits fell outside ± 3 dB, threshold was recalculated following sessions 3, 4, and 5, if necessary. The maximum number of sessions of this type for any frequency was five.

Aerial and underwater thresholds were obtained at each of the frequencies for each of the animals shown in Tables I and II. Occasionally, data from the initial method of constants sessions were considered unreliable because of unacceptable variability in testing behavior. In these cases, thresholds were determined following a minimum of 5 days testing, using the staircase method. Calculations of threshold and standard deviation were made using the method of Dixon and Mood (1948) for analyzing staircase data. Criteria for acceptable variability were the same as for the method of constant stimuli.

II. RESULTS

Aerial threshold estimates and false alarm rates (during sessions used for threshold determination) for each subject are shown in Table I, and these thresholds are graphically displayed in Fig. 1. In air, the harbor seal was most sensitive at all frequencies, followed by the older sea lion and the elephant seal.

Underwater thresholds and false alarm data for all subjects are shown in Table II. These data are graphically displayed in Fig. 2. The underwater curve for the sea lion represents average thresholds obtained from both animals

TABLE I. Aerial sound detection thresholds (in dB *re*: 20 μ Pa) and false alarms (in percent of catch trials) for Rocky (*Zalophus californianus*), Sprouts (*Phoca vitulina*), and Burnyce (*Mirounga angustirostris*).

| Frequency (Hz) | | Rocky (<i>Zalophus</i>) | Sprouts (<i>Phoca</i>) | Burnyce (<i>Mirounga</i>) |
|----------------|-----------|---------------------------|--------------------------|-----------------------------|
| 100 | Threshold | 77.5 | 65.4 | 78.6 |
| | FA | 15.0 | 6.0 | 3.3 |
| 200 | Threshold | 57.5 | 57.2 | 72.0 |
| | FA | 17.3 | 11.9 | 2.5 |
| 400 | Threshold | 59.2 | 52.9 | 68.8 |
| | FA | 10.5 | 3.3 | 9.5 |
| 800 | Threshold | 63.1 | 26.1 | 57.3 |
| | FA | 13.3 | 6.7 | 5.7 |
| 1600 | Threshold | 56.9 | 42.8 | 55.3 |
| | FA | 3.3 | 11.6 | 11.1 |
| 3200 | Threshold | 48.1 | 30.2 | 52.7 |
| | FA | 8.8 | 4.1 | 3.2 |
| 6400 | Threshold | 31.4 | 19.2 | 43.5 |
| | FA | 5.4 | 2.8 | 4.1 |

tested. In general, the elephant seal was most sensitive to underwater sound, followed by the harbor seal and the California sea lion. The elephant seal and harbor seal curves cross at just over 1000 Hz, but thresholds at the highest frequency tested (6300 Hz for the elephant seal and 6400 Hz for the harbor seal) are similar. Each curve shows a trend of generally increasing sensitivity from lower to higher frequencies. The two phocid curves are similar except in the vicinity of 200 to 400 Hz, where the elephant seal is about 10 dB more sensitive. The curve for the sea lion shows relatively poor hearing at frequencies below 1000 Hz. All three species exhibited similar sensitivity between 1000 and 6400 Hz.

Comparisons of aerial and underwater pressure thresholds corrected for reference level but not for impedance differences are shown in Fig. 3(A). Aerial pressure thresholds for the sea lion average 14 dB lower than underwater thresholds from the same animal, with the 1600-Hz threshold being nearly identical in both media. Pressure thresholds for the harbor seal are much more similar, with relatively minor differences (averaging 8 dB), except for the 800-Hz thresholds in which aerial sensitivity is nearly 30 dB greater than underwater sensitivity. For the elephant seal, aerial thresholds are greater than underwater thresholds for all frequencies tested. The differences in this case average 15 dB. Figure 3(B) shows the same comparisons but in this case sound-pressure levels have been converted to sound intensity levels, to correct for the impedance difference between air and water. Intensity thresholds for all the subjects are higher in air than in water, with average differences being 21, 27, and 51 dB for the sea lion, harbor seal, and elephant seal, respectively.

III. DISCUSSION

A. Near-field sensitivity

The low-frequency audiograms obtained from these subjects show a typical mammalian form (Fay, 1988). However,

TABLE II. Underwater sound detection thresholds (in dB re: 1 μ Pa) and false alarms (in percentage of catch trials) for Rocky and Rio (*Zalophus californianus*), Sprouts (*Phoca vitulina*), and Burnyce (*Mirounga angustirostris*).

| Frequency (Hz) | | Rocky (<i>Zalophus</i>) | Rio (<i>Zalophus</i>) | Sprouts (<i>Phoca</i>) | Burnyce (<i>Mirounga</i>) |
|----------------|-----------|---------------------------|-------------------------|--------------------------|-----------------------------|
| 75 | Threshold | 120.6 | 111.9 | 101.9 | 98.3 |
| | FA | 13.3 | 3.9 | 2.3 | 1.1 |
| 100 | Threshold | 119.4 | 116.3 | 95.9 | 89.9 |
| | FA | 6.6 | 10.0 | 5.3 | 2.6 |
| 200 | Threshold | 103.7 | 100.1 | 83.8 | 72.8 |
| | FA | 4.0 | 12.0 | 7.9 | 3.9 |
| 400 | Threshold | 100.0 | 88.9 | 83.9 | 74.9 |
| | FA | 11.1 | 4.7 | 8.8 | 4.1 |
| 800 | Threshold | 105.6 | 84.2 | 79.8 | 73.5 |
| | FA | 3.3 | 2.9 | 10.1 | 3.6 |
| 1600 | Threshold | 78.7 | 69.3 | 67.1 | 73.4 |
| | FA | 6.5 | 8.0 | 3.3 | 2.2 |
| 3200 | Threshold | | | | 73.3 |
| | FA | | | | 3.4 |
| 6300 | Threshold | | | | 59.0 |
| | FA | | | | 2.7 |
| 6400 | Threshold | 79.8 | 57.1 | 62.8 | |
| | FA | 3.3 | 10.2 | 6.0 | |

the sea lion's 75-Hz thresholds deviate from the expected monotonic low-frequency up-slope. The younger sea lion's threshold at 75 Hz is 3 dB lower than her threshold at 100 Hz while that of the older is no higher than her threshold at 100 Hz. This is particularly noteworthy considering that the two phocid audiograms show a fairly steep rise below 100 Hz. It is likely that the low thresholds at 75 Hz for the two sea lions resulted from a sensory modality shift (sound detection to vibration detection). Turl (1993) found a similar effect in dolphins at low frequencies which he attributed to sensation of particle motion. Close to the projector, especially with long test wavelengths, such an effect is likely because of the high amplitude of particle movements associated with the

near field (Siler, 1969). Close to the sound source, hydrodynamic flow dominates the sound field, and effects other than pressure (particle motion) can be responsible for sensation of a test stimulus. Beyond the near field, the effects of particle motion are less noticeable, as the ratio of pressure to particle velocity approaches that of a plane wave (Siler, 1969; Rogers and Cox, 1988). If the subject was able to sense particle motion in the near field, then it may report a signal, even if the measured sound pressure of the stimulus was at or below ambient noise levels. Turl (1993) found that after an initial response plateau corresponding to thresholds obtained for

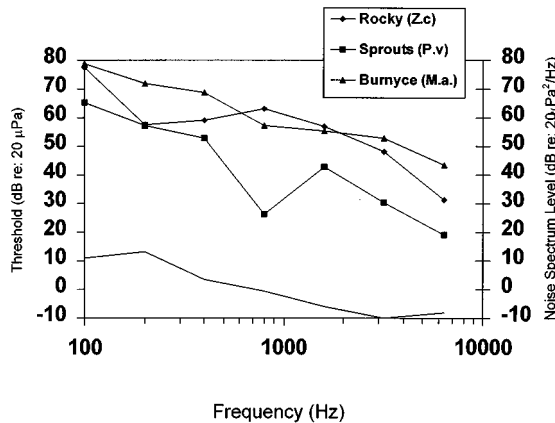


FIG. 1. Aerial sound detection thresholds (100–6400 Hz) and typical noise spectrum levels recorded beneath the headphones (at the level of the external meatal opening) for *Zalophus*, *Phoca*, and *Mirounga*.

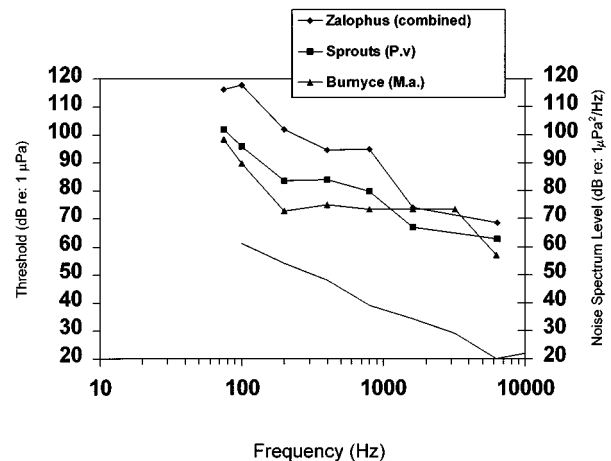


FIG. 2. Underwater sound detection thresholds (75–6400 Hz) and typical noise spectrum levels recorded at the chin station for *Zalophus* (average of two animals), *Phoca*, and *Mirounga*.

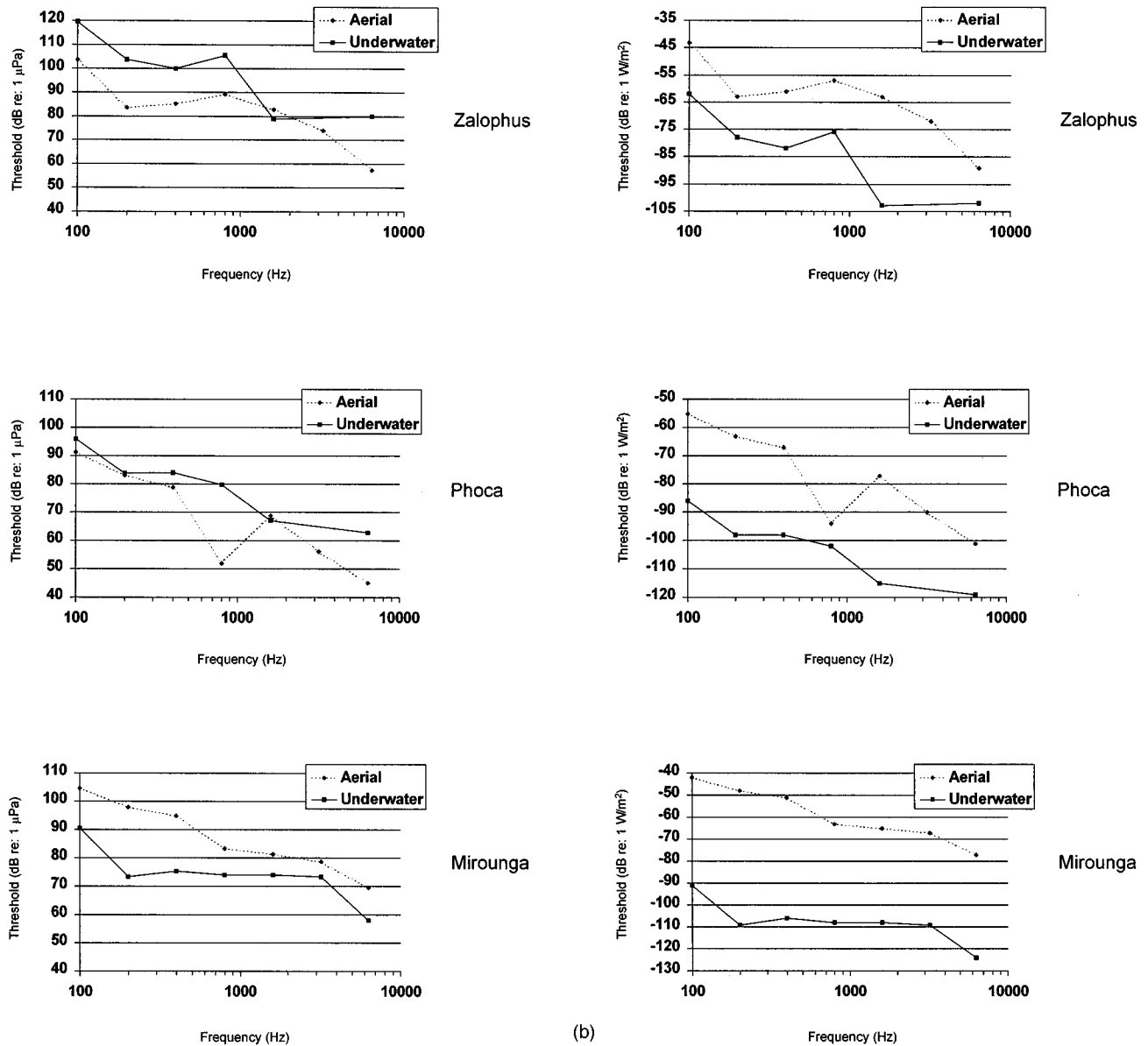


FIG. 3. Comparisons of aerial and underwater sound-pressure detection thresholds (A) and sound intensity thresholds (B) for *Zalophus*, *Phoca*, and *Mirounga*. Aerial thresholds have been corrected with respect to reference level (converted from 20 to 1 μPa). Underwater thresholds were estimated using the pressure/intensity relationship for a plane progressive wave in the far field.

Tursiops by Johnson (1967), his dolphin began responding to signal levels at sound-pressure levels below that of the ambient noise.

The sea lions in this study likely responded in the same way. The wavelength of a 75-Hz signal produced underwater is 20 m, and the approximate near-field–far-field boundary (Siler, 1969) is $\lambda/2\pi$ or 3.18 m. Although the separation of projector and chin station in these experiments was on the order of 5 m, the distinction between near and far field in the reverberant enclosure is not as clear cut, and significant deviations from expected magnitudes of particle motion were likely present outside the predicted near field (Fahy, 1989). It is thus likely that the drop in threshold at 75 Hz is due to sensation of particle motion, possibly by the sea lions' vibrissae, an effect that should be more evident with increasing wavelength. This conclusion is supported by the fact that Rocky, the older of the two sea lions, had considerable dif-

ficulty with this frequency, yet responded more often than not at stimulus levels lower than expected based on her 100-Hz threshold. The modality shift (hearing to feeling) probably caused considerable confusion for this subject.

Of further interest is the fact that neither of the phocids responded in a similar way to the 75-Hz signal. There are two possible explanations for this lack of response. The first is that neither seal was sensitive to particle motion; therefore both responded solely to auditory stimulation. This is unlikely given the bulk of anatomical and behavioral work on seal vibrissae (Renouf, 1979, 1980; Hyvaarinen, 1989) which suggests that the vibrissae are sensitive to minute near-field displacements. The second explanation is that particle motion as a cue was overshadowed by auditory cues. Whatever the case, particle motion associated with the acoustic near field appeared to control the behavior of both California sea lions and therefore might be used as a cue to

detect the presence of swimming prey at close range (Renouf, 1980).

B. Air–underwater comparisons

In order for an auditory threshold to be biologically meaningful, it must take into consideration the particular stimulus detected by the animal in nature. Thus there is some concern about whether to use sound pressure or intensity to compare aerial versus underwater hearing sensitivity. For instance, Lombard *et al.* (1981) concluded that the appropriate measure of comparison between aerial and underwater hearing in the bullfrog (*Rana catesbeiana*) is intensity. The rationale for this conclusion was that at the time, sufficient evidence that the frog ear operates in a similar fashion in both media did not exist. Because Lombard *et al.* did not think they could justify a pressure mode of underwater sound reception they compared aerial and underwater thresholds in terms of intensity. However, in a subsequent paper (Hetherington and Lombard, 1982) it was shown that under water, the ears of several frog species responded to pressure rather than particle motion. If one can reasonably assume similarity of aerial and underwater functioning of the ear, then comparisons should be made on the basis of the relevant parameter, in this case, acoustic pressure. Intensity comparisons based solely on accepted practice do little to shed light on the physiological nature of the detection process, and indeed, imply that the auditory system of amphibious animals functions differently underwater than in air.

There are various reasons to suspect that the sound pressure is conducted through the pinniped middle ear under water. Møhl and Ronald (1975) found that the optimal site for sound entry under water was over the external meatus, suggesting that it acts as an acoustic waveguide (see also Ramprashad, 1975). Additionally, experiments by Møhl and Ronald (1975) suggest that the effective interaural distance corresponds to the span between the outer ear openings rather than the separation of the inner ears. These investigators also reported that the auditory reflex could be induced underwater by loud sounds (with a corresponding 10-dB increase in threshold), again suggesting that the middle ear is functional in water. Though these data do not eliminate the possibility that bone conduction of acoustic particle motion occurs, they do indicate a preferential sound pathway similar to the one used in air. Ramprashad (1975) suggested that the sound pathway may be the walls or lumen of the external meatus, and that the inner ear might be stimulated via pressure fluctuations in the middle ear (either via the ossicles or directly through the middle ear cavity). In this respect it is interesting that there is a spatial separation of the round and oval windows in the phocids (Repenning, 1972). This separation may be an adaptation for receiving sound directly through the middle ear, functioning to maintain a high acoustic pressure difference between the oval and round windows. This pressure difference is the primary stimulus for auditory sensation in conventional hearing (Voss *et al.*, 1996).

It is possible that under water, pressure waves stimulate the pinniped inner ear in one or more of five primary ways: (1) via direct ossicular action, given that the ossicles function normally in a middle ear space of increased air density, or

surrounded by cavernous tissue; (2) direct window stimulation through the middle ear cavity, with little loss due to the good impedance match between the cavernous tissue and water along with the separation of the oval and round windows; (3) via the middle ear cavity air space which should vibrate under pressure fluctuations, transmitting particle displacements to the inner ear (Lipatov, 1992, inferred a similar function for the air-filled external meatus); (4) via the skull, through translational bone conduction, in which pressure fluctuations cause the skull and tympanic bones to vibrate around the ossicles; or (5) direct compression of the cochlear capsules via bone conduction. With respect to (2) above, the relatively low ratio between the tympanic membrane and the oval window in pinnipeds is thought to be an adaptation to protect the inner ear from the generally greater sound-pressure levels underwater (Repenning, 1972). Thus the spatial separation of the oval window and round window may serve two functions, (1) to maintain the pressure difference between the two windows when sound waves impinge upon the middle ear; and (2) to shield the round window from the corpus cavernosum at depth, in order to maintain its compliance.

There has been considerable interest in the route of sound conduction to the pinniped inner ear since the first air/water comparisons were made (Møhl, 1968b). The acoustic impedance difference between air and water is typically used to predict a 30-dB loss in sensitivity (with respect to intensity) underwater for an air adapted ear and vice versa. Such a view of the ear as an air/water interface appears to be an oversimplification. Because the pinniped head ought to be acoustically transparent or nearly so under water, it is often stated that sound energy enters the inner ears via the skull and head tissues. However, Møhl and Ronald (1975) experimentally rejected the idea of an acoustically transparent head under water. Additionally, pinniped underwater hearing sensitivity cannot be explained on the basis of vibration of the skull by particle motion in the acoustic far field, especially at high frequencies. The amplitude of acoustic particle motion at a particular pressure threshold should not be sufficient to cause sensation, even if were transmitted without attenuation to the inner ear. For instance, at a distance of 5 m from a sound source, the particle displacement corresponding to a pressure level of 60 dB *re*: 1 μ Pa at 6400 Hz (elephant seal threshold) is on the order of 10^{-5} nm (Harris and van Bergeijk, 1962). Given that at threshold, hair-bundle deflection is on the order of 0.3 nm (Hudspeth, 1989), it is extremely unlikely that particle motions associated with underwater sound at any significant distance from the source (i.e., far field) are responsible for sensation by the mammalian ear. Rather, acoustic pressure is likely to be the predominant stimulus. It is known that fish with pressure transducers (swim bladders) have an acoustic advantage in frequency range as well as absolute sensitivity over fish without such transducers (Popper and Fay, 1993). By exploiting acoustic pressure, these fish are able to detect sound sources at much greater ranges than predicted on the basis of sensitivity to particle motion alone. It is extremely likely that pinnipeds as well as cetaceans are sensitive to acoustic pressure under water, because patterns of auditory sensitivity in these ma-

rine mammals reflect an expanded frequency range and a high degree of sensitivity. These characteristics are not seen in organisms sensitive strictly to acoustic particle motion. Clearly, experiments in which pressure and particle motion can be spatially separated are needed to confirm this suggestion. Until such experiments are conducted we can only speculate on sound conduction pathways, relative sensitivity to pressure versus particle motion, and the amphibious adaptations of the middle ear.

In addition to the theoretical matters, there are practical concerns when determining whether to compare auditory thresholds using pressure or intensity. Because of the acoustic properties of small test tanks, intensity calculations based on pressure measurements are likely to be *underestimates* (Parvulescu, 1964; Hetherington and Lombard, 1982). Ridgway *et al.* (1997) recently obtained sound detection thresholds in the open ocean. The beluga whale (*Delphinapterus leucas*) pressure thresholds in this study were similar to those obtained by Awbrey *et al.* (1988) and Johnson *et al.* (1989) in a test tank and a shallow-water pen, respectively. However, the intensity values calculated from pressure in the latter two studies (tanks or shallow-water situations) are probably inaccurate. Intensity values calculated from pressure in the open ocean study should more closely conform to the $p^2/\rho c$ relationship. Thus *similar* pressure thresholds among the various belugas tested are highly likely to correspond to *different* intensity thresholds which are based solely on the configuration of the test tank and not on the receiving characteristics of the animals. In fact, intensity thresholds may be specific to various experimental procedures (e.g., presence of reflective boundaries), whereas pressure thresholds are relatively independent of such factors, provided that the sound fields are carefully mapped. Accurate estimates of intensity are impossible to obtain from earlier marine mammal studies, without making unwarranted assumptions about the acoustic characteristics of the testing configuration.

Similar tests at depth with seals and sea lions will be necessary to draw firm conclusions regarding sound reception by the pinniped ear. As in the beluga, comparable hearing thresholds in tanks, shallow open water, and at depth would be indicative of pressure detection.

Finally, aerial/underwater hearing data obtained from an essentially terrestrial mammal, the human, have been compared in terms of pressure rather than intensity in 11 out of 12 studies reviewed by Kirkland *et al.* (1989). Based on a thorough consideration of the evidence as well as standard practice, we believe that pressure is the relevant parameter to use when examining underwater hearing in marine mammals.

C. Low-frequency sound and anthropogenic noise

The low-frequency thresholds obtained from these subjects suggest that the California sea lion is relatively insensitive to the frequencies associated with most types of anthropogenic sound in the ocean. At frequencies around 100 Hz the sea lion's threshold appears to be much higher than typical sources of man-made noise at moderate distances from the source.

The harbor seal is about 20 dB more sensitive to signals at 100 Hz than the California sea lion. It is thus more likely to hear low-frequency sounds from man-made sources such as ships and oil-drilling platforms. The effects of such sounds, if heard, are unknown, but potentially deleterious. For instance, harbor seal males produce low-frequency underwater sounds during the breeding season (Hanggi and Schusterman, 1994). It is possible that even if no behavioral reaction to anthropogenic noise is evident, masking of intraspecific signals may occur.

The elephant seal is the most sensitive to underwater low-frequency sound. It is thus most likely to hear low-frequency noise, but, as in other pinnipeds, the effects of such sounds are unknown. A potential factor to consider when assessing the possible effects of sound on elephant seals is that these animals are routine deep divers (LeBoeuf *et al.*, 1988). Dives to or below the deep sound channel may expose these animals to higher sound levels than would be predicted based on simple propagation models. In addition, there is some evidence that elephant seals (in contrast to sea lions and harbor seals) do not readily habituate to certain types of sound (Schusterman and Kastak, 1996), but may actually become sensitized not only to disturbing noises, but to environmental features associated with the noises.

Firm conclusions cannot be drawn regarding the effects of noise on animals, even when thresholds are known. It is possible, however, to calculate ranges of detectability for different types of sound sources. For instance, the sound used by the Acoustic Thermometry of Ocean Climate project (ATOC) has a source pressure level of 195 dB *re*: 1 μ Pa and a center frequency of 75 Hz. Ranges of detection estimated by assuming a simplified propagation model of spherical spreading ($20 \log R$) to a distance of 1000 m followed by 15 $\log R$ (or "lossy" cylindrical) spreading, and the 75 Hz thresholds listed in Table II are approximately 9–34 km for a California sea lion, 160 km for a harbor seal, and 279 km for an elephant seal. Based on ocean noise measurements cited in Richardson *et al.* (1995), detection of the signal by these animals could be limited to shorter ranges at sea states of about four or higher, or in the presence of shipping or other noise (assuming critical ratios at 75 Hz to be over 20 dB). Although this simplified example does not take into account real propagation effects, it offers an illustration of how sensitivity differences might reflect differences in susceptibility to the effects of anthropogenic noise.

The presumed functioning of the middle ear as an underwater pressure transducer has important implications regarding the predictions related to both tolerable levels of sound and the physical acoustic parameters that should be used when comparing underwater sounds (such as ATOC) with their airborne counterparts. For example, as evidenced by the recent ATOC controversy, the corrections for intensity and reference levels between airborne and underwater sound has led physical acousticians and scientists dealing with the public to simply "subtract 60 dB" from underwater sound levels to convert to a scale purportedly comparable to the in-air scale more familiar to the public. Such a translation not only neglects the characteristics of underwater auditory systems (such as the pinniped ear), but is misleading because

TABLE III. Average differences between aerial and underwater sound detection thresholds for three phocid species, two otariid species, and one odontocete cetacean (bottlenose dolphin—*Tursiops truncatus*). Thresholds are compared with respect to pressure (column 4), corrected for reference level, and intensity (column 5), calculated from pressure measurements using $I = p^2/\rho c$. Positive values indicate greater sensitivity (lower thresholds) underwater; negative values indicate greater sensitivity in air.

| Family | Species | N | Avg. pressure difference (dB) | Avg. intensity difference (dB) | References |
|-------------|--------------------------------|---|-------------------------------|--------------------------------|---|
| Phocidae | <i>Phoca vitulina</i> | 3 | -10.1 | 25.6 | Mohl, 1968a; Terhune, 1989, 1991; this study |
| Phocidae | <i>Phoca groenlandica</i> | 1 | -8.3 | 27.4 | Terhune and Ronald, 1971, 1972 |
| Phocidae | <i>Mirounga angustirostris</i> | 1 | 15.9 | 51.6 | This study |
| Otariidae | <i>Zalophus californianus</i> | 3 | -23.6 | 12.1 | Schusterman <i>et al.</i> , 1972; Schusterman, 1974; this study |
| Otariidae | <i>Callorhinus ursinus</i> | 3 | -27.0 | 8.7 | Babushina <i>et al.</i> , 1991; Moore and Schusterman, 1987 |
| Delphinidae | <i>Tursiops truncatus</i> | 1 | 23.5 | 59.2 | Babushina, 1979 |

it artificially reduces (by 60 dB) the presumed amplitude of such stimuli. While these conversions are defensible from a strictly physical standpoint, they fail to address the relevant biological issues involved in the detection of underwater sound by marine animals. Without an understanding of the hearing abilities of these animals (i.e., complete audiometric assessment), perhaps the best approach is to estimate sound exposure levels based on a “best guess” as to the functioning of the particular auditory systems involved. We believe that from both a physiological and ecological viewpoint, the appropriate approach for comparing aerial and underwater hearing in pinnipeds should take into consideration sound-pressure levels rather than, or in addition to, sound intensity levels. Figure 3(A) and (B) illustrates the differences between these two comparisons, as well as between the conclusions drawn independently from each measure (e.g., using the intensity comparison, the sea lion ear appears “water-adapted” while using the pressure comparison it appears “air-adapted”).

D. Comparative aspects

Previous intensity comparisons of other otariids were used as evidence that the otariid ear is “water-adapted” (Moore and Schusterman, 1987; Babushina *et al.*, 1991). Paradoxically, a study of otariid ear morphology reveals what are considered to be only minor modifications for sound reception underwater (King, 1983). When aerial and underwater thresholds are compared in terms of pressure, however, this lack of aquatic adaptation is clear. For the sea lion tested in both media, the aerial thresholds obtained in this study average 14 dB better than the underwater thresholds. From an adaptive standpoint, this implies that efficient aerial functioning is necessary for this species, and it has sacrificed some degree of aquatic adaptation in order to retain aerial sensitivity.

Compared to the otariids, *Phoca* has a more extreme sensitivity bias underwater when viewed in terms of sound intensity. These differences, on the order of 15–30 dB (Mohl, 1968b; Terhune, 1989, 1991) suggest an ear highly adapted to hearing underwater. When viewed in terms of

pressure, however, the similarity of aerial and underwater thresholds obtained for the *Phoca* in this study is striking. The only great difference in sensitivity occurs at 800 Hz, and is due to the presence of a notch at this frequency in the aerial audiogram. The notch is suggestive of a resonance in the external auditory meatus. The similarity between pressure thresholds in the two media strongly suggests that, as Møhl (1968b) and others have hypothesized, the harbor seal has maximized both aerial and underwater hearing sensitivity. Absolute aerial thresholds are higher than those of most terrestrial carnivores, and underwater thresholds are higher than those of strictly aquatic mammals (e.g., cetaceans), when comparing within the range of best sensitivity.

The pressure comparisons for *Mirounga* strengthen the conclusion that the elephant seal is water-adapted. In each case, the aerial threshold is greater than the corresponding underwater threshold. From a morphological standpoint, the elephant seal ear does not appear well adapted to detect aerial acoustic signals. The external meatus is long, narrow, and closed, despite the presence of musculature attached to its cartilaginous supporting structures. It is highly unlikely that a continuous air space exists between the environment and the tympanic membrane, a necessity for efficient aerial hearing. In addition, the tympanic membrane-oval window ratio is on the order of 10:1 (Repenning, 1972), probably conferring protection from sound pressure underwater, but extremely inefficient for pressure amplification in air.

Using results from the present study and those of earlier investigations, we compared the aerial and underwater hearing sensitivity of certain phocids and otariids. These are summarized in Table III (which includes data from five phocid seals, five otariid seals, and one odontocete cetacean). These comparisons are quite revealing in demonstrating that differences in sensitivity are less variable within families than between families. The elephant seal data from Table III are significantly different at the 0.05 level (Tukey–Kramer HSD) from that of each of the other pinnipeds, and the relative differences between aerial and underwater hearing in this subject corroborate predictions based on gross morphology and ecology. Interestingly, the elephant seal data are not

TABLE IV. Ecological factors likely to have influenced low-frequency aerial and underwater hearing sensitivity in the California sea lion (*Zalophus californianus*), the harbor seal (*Phoca vitulina*), and the northern elephant seal (*Mirounga angustirostris*). Pluses indicate the relative degree to which each factor is present in each species (e.g., *Zalophus* is extremely vocal in air).

| | <i>Zalophus</i> | <i>Phoca</i> | <i>Mirounga</i> |
|-----------------------------|----------------------------|--|---------------------------|
| Aerial sound production | +++ moderate–high freq. | + low freq. | +++ low freq. (adults) |
| Underwater sound production | + broadband | +++ low freq./broadband | ? |
| Time spent at sea | + | ++ | +++ |
| Deep dives | shallow | ? (most shallow; some evidence of deep dives) | +++ |

significantly different from that of the bottlenose dolphin, an odontocete presumably well adapted to hear underwater and poorly adapted to hear in air. The similarities imply a convergence in medium-specific auditory sensitivity between the two species; however, much more data must be collected from each species both in air and underwater in order to strengthen the conclusions based on these comparisons.

Table III also shows the same data when comparisons are made with respect to intensity rather than pressure. While the trends among family groupings are similar, the degree of aquatic adaptation appears dramatically different using such comparisons. All pinniped ears, regardless of phylogenetic relationship or life history appear water adapted when intensity is used to compare aerial and underwater hearing. While this may be somewhat informative from a physical standpoint, it fails to reveal what we believe are the appropriate relationships between life history, ecology, and amphibious hearing that emerge when comparisons are made with respect to pressure.

The elephant seal appears to be an aquatic specialist. Auditory sensitivity for this species is greater underwater regardless of whether pressure or intensity is used as a measure of comparison. These extreme modifications likely reflect the elephant seal's ability to dive regularly to depths of 500–700 m (LeBoeuf *et al.*, 1989). The external meatus, already closed in air, essentially disappears upon submergence to even shallow depths. The air normally occupying the middle ear space should yield to corpus cavernosum as pressure increases from 1 atm at the surface to over 100 atm at maximum dive depths.

The nearly complete closure of the external meatus decreases the aerial hearing sensitivity of *Mirounga* relative to other pinnipeds. However, aerial vocalizations produced by elephant seals are exceptionally loud, and are highly correlated with visual and seismic cues (Shipley *et al.*, 1992). Thus although the elephant seal has relatively poor aerial sensitivity, it has compensated to allow effective aerial communication.

Table IV shows the ecological factors that are likely involved in hearing, specifically at low frequencies. The tendencies illustrated by this table suggest that *Zalophus* should

have the best aerial hearing sensitivity, followed by *Phoca*, then *Mirounga*. If underwater hearing is related to deep diving and the overall amount of time spent at sea, then *Mirounga* ought to be the most sensitive to underwater sound, followed by *Phoca*, then *Zalophus*. Overall, both *Mirounga* and *Phoca* should have good low-frequency hearing, followed by *Zalophus*.

Thus, from an ecological standpoint, the results of this study come as no surprise; *Zalophus* relies on aerial communication to a greater extent than the other species, in that it must recognize subtle signal characteristics involved in such aerial vocalizations as pup attraction calls (Gisiner and Schusterman, 1991; Schusterman *et al.*, 1992). In addition, most sea lion vocal signals have greatest intensities at 1000 Hz or higher (Peterson and Bartholomew, 1969; Schusterman, 1978), so low-frequency hearing might be expected to be relatively poor.

The harbor seal produces aerial vocalizations, but it is unclear to what extent subtle differences in signal content are detected and utilized. Harbor seal pups call simultaneously in air and underwater, thus good amphibious hearing is indicated. Apart from the pup calls, harbor seal vocalizations are either broadband clicking or creaking sounds, or low-frequency, guttural roars (Hanggi and Schusterman, 1994). Harbor seals, therefore, are expected to have relatively good low-frequency hearing and relatively good underwater hearing.

The northern elephant seal produces loud low-frequency vocalizations in air (Bartholomew and Collias, 1962). Although Poulter (1968) claims to have recorded underwater vocalizations from the northern elephant seal, evidence for this occurrence is sparse (Fletcher *et al.*, 1996). At this point it is difficult to determine whether the underwater sensitivity of the elephant seal is related to adaptive pressures to hear well under water, or to pressure-compensate at depth, or both.

IV. SUMMARY

As a group, the pinnipeds have exploited the aquatic environment but have remained tied to the shore. Retention

of the sensitivity of one sensory modality in air places constraints upon the ability of this sense to function well underwater. The phylogenetic constraints of the fissiped ear remain present to some extent in all members of this group. The hearing mechanism has been modified by the selective pressures brought about by the life histories of each species. This is most evident within the phocids, and can be seen in a comparison of the aerial and underwater hearing abilities of two species with drastically different ecologies, the harbor seal and northern elephant seal. Additional work on the sound reception pathways, hearing at depth, absolute sensitivities, frequency discrimination, sound localization, and masking in all species is needed before any more firm conclusions are drawn from behavioral data.

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