# NOAA Technical Memorandum NMFS



SEPTEMBER 1998

# MARINE MAMMAL AUDITORY SYSTEMS: A SUMMARY OF AUDIOMETRIC AND ANATOMICAL DATA AND ITS IMPLICATIONS FOR UNDERWATER ACOUSTIC IMPACTS

Darlene R. Ketten, Ph. D.

NOAA-TM-NMFS-SWFSC-256

U.S. DEPARTMENT OF COMMERCE
National Oceanic and Atmospheric Administration
National Marine Fisheries Service
Southwest Fisheries Science Center

The National Oceanic and Atmospheric Administration (NOAA), organized in 1970, has evolved into an agency which establishes national policies and manages and conserves our oceanic, coastal, and atmospheric resources. An organizational element within NOAA, the Office of Fisheries is responsible for fisheries policy and the direction of the National Marine Fisheries Service (NMFS).

In addition to its formal publications, the NMFS uses the NOAA Technical Memorandum series to issue informal scientific and technical publications when complete formal review and editorial processing are not appropriate or feasible. Documents within this series, however, reflect sound professional work and may be referenced in the formal scientific and technical literature.

Southwest Fisheries Science Center
P.O. Box 271
La Jolla, California 92038-0271

June 11, 1999

The enclosed "Table 1. Marine Mammal Sound Production Characteristics" is a replacement for Table 1 in the 1998 NOAA Technical Memorandum titled *Marine Mammal Auditory Systems: A Summary of Audiometric and Anatomical Data and Its Implications for Underwater Acoustic Impacts*" by Darlene R. Ketten (NOAA-TM-NMFS-SWFSC-256). Dr. Ketten noted the original table data for *Phoca vitulina* and *Phoca largha*, are reversed. The revised table corrects this error and includes data for a few additional species.

Thank you for your interest and assistance in these investigations.

Sincerely,

Chuck Oliver

coliver@sgilj.ucsd.edu
619-546-7172 (voice)
619-546-7003 (fax)

Table 1. Marine Mammal Sound Production Characteristics

(Data compiled from Popper 1980; Watkins and Wartzok 1985; Ketten 1992; Au 1993; Richardson *et al.* 1995; Ketten 1997)

| Scientific Name | Common Name | Signal Type | Frequency Range (kHz) | Frequency at Maximum Energy (kHz) | Source Level (dB re 1 μPa) | References |
|---|---|---|---|---|---|---|
| Cetacea | | | | | | |
| Odontoceti | | | | | | |
| Delphinidae | | | | | | |
| *Cephalorhynchus commersonii* | Commerson's dolphin | pulsed sounds | <10 | 0.2-5 | - | Watkins and Schevill 1980; Dziedzic and de Buffrenil 1989 |
| | | clicks | - | 6 | - | Dziedzic and de Buffrenil 1989 |
| | | click | - | 116-134 | 160 | Kamminga and Wiersma 1981; Shochi *et al.* 1982; Evans *et al.* 1988; Au 1993 |
| *Cephalorhynchus heavisidii* | Heaviside's dolphin | pulsed sounds | 0.8-5[a] | 0.8-4.5[a] | - | Watkins *et al.* 1977 |
| | | click | - | 2-5 | - | Watkins *et al.* 1977 |
| *Cephalorhynchus hectori* | Hector's dolphin | click | - | 112-135 | 150-163 | Dawson 1988; Dawson and Thorpe 1990; Au 1993 |
| *Delphinus delphis* | Common dolphin | whistles, chirps, barks | - | 0.5-18 | - | Caldwell and Caldwell 1968; Moore and Ridgway 1995 |
| | | whistles | 4-16 | - | - | Busnel and Dziedzic 1966a |
| | | click | 0.2-150 | 30-60 | - | Busnel and Dziedzic 1966a |
| | | click | - | 23-67 | - | Dziedzic 1978 |
| *Feresa attenuata* | Pygmy killer whale | growls, blats | - | - | - | Pryor *et al.* 1965 |
| *Globicephala macrorhynchus* | Short-finned pilot whale | whistles | 0.5->20 | 2-14 | 180 | Caldwell and Caldwell 1969; Fish and Turl 1976 |
| | | click | - | 30-60 | 180 | Evans 1973 |
| *Globicephala melaena* | Long-finned pilot whale | whistles | 1-8 | 1.6-6.7[b] | - | Busnel and Dziedzic 1966a |
| | | clicks | 1-18 | - | - | Taruski 1979; Steiner 1981 |
| | | click | - | 6-11 | - | McLeod 1986 |
| *Grampus griseus* | Risso's dolphin | whistles | - | 3.5-4.5 | - | Caldwell *et al.* 1969 |
| | | rasp/pulse burst | 0.1-8[c] | 2-5 | - | Watkins 1967 |
| | | click | - | 65 | ~120 | Au 1993 |
| *Lagenodelphis hosei* | Fraser's dolphin | whistles | 7.6-13.4 | - | - | Leatherwood *et al.* 1993 |

| | | | | | | |
|---|---|---|---|---|---|---|
| *Lagenorhynchus acutus* | Atlantic white-sided dolphin | whistles | - | 6-15[b] | - | Steiner 1981 |
| *Lagenorhynchus albirostris* | White-beaked dolphin | squeals | - | 8-12 | - | Watkins and Schevill 1972 |
| *Lagenorhynchus australis* | Peale's dolphin | pulses (buzz) | 0.3-5 | 0.3 | - | Schevill and Watkins 1971 |
| | | clicks | to 12 | to 5 | low | Schevill and Watkins 1971 |
| *Lagenorhynchus obliquidens* | Pacific white-sided dolphin | whistles | 2-20 | 4-12 | - | M. Caldwell and Caldwell 1971 |
| | | click | - | 60-80 | 180 | Evans 1973 |
| *Lagenorhynchus obscurus* | Dusky dolphin | whistles | 1.0-27.3 | 6.4-19.2[b] | - | Wang Ding *et al.* 1995 |
| *Lissodelphis borealis* | Northern right whale dolphin | whistles, tones | 1-16 | 1.8, 3 | - | Leatherwood and Walker 1979 |
| *Orcinus orca* | Killer whale | whistles | 1.5-18 | 6-12 | - | Steiner *et al.* 1979; Ford and Fisher 1983; Morton *et al.* 1986 |
| | | click | 0.25-0.5 | - | - | Schevill and Watkins 1966 |
| | | scream | 2 | - | - | Schevill and Watkins 1966 |
| | | click | 0.1-35 | 12-25 | 180 | Diercks *et al.* 1971, Diercks 1972 |
| | | pulsed calls | 0.5-25 | 1-6 | 160 | Schevill and Watkins 1966; Awbrey *et al.* 1982; Ford and Fisher 1983; Moore *et al.* 1988 |
| *Pseudorca crassidens* | False killer whale | whistles | - | 4-9.5 | - | Busnel and Dziedzic 1968; Kamminga and van Velden 1987 |
| | | click | | 25-30; 95-130 | 220-228 | Kamminga and van Velden 1987; Thomas and Turl 1990 |
| *Sotalia fluviatilis* | Tucuxi | whistles | 3.6-23.9 | 7.1-18.5[b] | - | Wang Ding *et al.* 1995 |
| | | click | - | 80-100 | high | Caldwell and Caldwell 1970; Norris *et al.* 1972; Kamminga *et al.* 1993 |
| *Sousa chinensis* | Humpback dolphin | whistles | 1.2-16 | - | - | Schultz and Corkeron 1994 |
| *Stenella attenuata* | Spotted dolphin | whistles | 3.1-21.4 | 6.7-17.8[b] | - | Wang Ding *et al.* 1995 |
| | | whistles | - | - | - | Evans 1967 |
| | | pulse | to 150 | - | - | Diercks 1972 |
| *Stenella clymene* | Clymene dolphin | whistles | 6.3-19.2 | - | - | Mullin *et al.* 1994 |
| *Stenella coeruleoalba* | Spinner dolphin | whistles | 1-22.5 | 6.8-16.9[b] | 109-125 | Watkins and Schevill 1974; Steiner 1981; Norris *et al.* 1994; Wang Ding *et al.* 1995 |

| | | | | | | |
|---|---|---|---|---|---|---|
| | | pulse bursts | wide band | 5-60 | 108-115 | Watkins and Schevill 1974; Norris *et al.* 1994 |
| | | screams | - | - | - | Norris *et al.* 1994 |
| *Stenella longirostris* | Long-snouted spinner dolphin | pulse | 1-160 | 5-60 | - | Brownlee 1983 |
| | | whistle | 1-20 | 8-12 | - | Brownlee 1983 |
| | | click | - | low-65 | - | Watkins and Schevill 1974; Norris *et al.* 1994 |
| | | click | 1-160 | 60 | - | Ketten 1984 |
| *Stenella plagiodon* | Spotted dolphin | whistles | 5.0-19.8 | 6.7-17.9[b] | - | M. Caldwell *et al.* 1973; Steiner 1981 |
| | | clicks | 1-8 | - | - | Caldwell and Caldwell 1971b |
| | | squawks, barks, growls, chirps | 0.1-8 | - | - | Caldwell *et al.* 1973 |
| *Stenella styx* | Gray's Porpoise | whistles | 6-24 | 8-12.5 | - | Busnel *et al.* 1968 |
| *Steno bredanensis* | Rough-toothed dolphin | whistles | - | 4-7 | - | Busnel and Dziedzic 1966b |
| | | click | - | 5-32 | - | Norris and Evans 1967 |
| *Tursiops truncatus* | Bottlenosed dolphin | whistles | 0.8-24 | 3.5-14.5[b] | 125-173 | Lilly and Miller 1961; Tyack 1985; Caldwell *et al.* 1990; Schultz and Corkeron 1994; Wang Ding *et al.* 1995 |
| | | rasp, grate, mew, bark, yelp | - | - | - | Wood 1953 |
| | | click | 0.2-150 | 30-60 | - | Diercks *et al.* 1971; Evans 1973 |
| | | bark | 0.2-16 | - | - | Evans and Prescott 1962 |
| | | whistle | 4-20 | - | - | Caldwell and Caldwell 1967; Evans and Prescott 1962 |
| | | click[d] | - | 110-130 | 218-228 | Au *et al.* 1974; Au 1993 |
| Monodontidae | | | | | | |
| *Delphinapterus leucas* | Beluga | whistles | 0.26-20 | 2-5.9 | - | Schevill and Lawrence 1949; Sjare and Smith 1986a, b |
| | | pulsed tones | 0.4-12 | 1-8 | - | Schevill and Lawrence 1949; Sjare and Smith 1986a,b |
| | | noisy vocalizations | 0.5-16 | 4.2-8.3 | - | Schevill and Lawrence 1949; Sjare and Smith 1986a,b |

| | | | | | | |
|---|---|---|---|---|---|---|
| | | echolocation click | | 40-60, 100-120 | 206-225 | Au *et al.* 1985, 1987; Au 1993 |
| *Monodon monoceros* | Narwhal | pulsed tones | 0.5-5 | - | - | Ford and Fisher 1978 |
| | | whistles | 0.3-18 | 0.3-10 | - | Ford and Fisher 1978 |
| | | click | - | 40 | 218 | Møhl *et al.* 1990 |
| Phocoenidae | | | | | | |
| *Neophocaena phocaenoides* | Finless porpoise | clicks | 1.6-2.2 | 2 | - | Pilleri *et al.* 1980 |
| | | click | - | 128 | - | Kamminga *et al.* 1986; Kamminga 1988 |
| *Phocoenoides dalli* | Dall's porpoise | clicks | 0.04-12 | - | 120-148 | Evans 1973; Evans and Awbrey 1984 |
| | | click | - | 135-149 | 165-175 | Evans and Awbrey 1984; Hatakeyama and Soeda 1990; Hatakeyma *et al.* 1994 |
| *Phocoena phocoena* | Harbour porpoise | clicks | 2 | - | 100 | Busnel and Dziedzic 1966a; Schevill *et al.* 1969 |
| | | pulse | 100-160 | 110-150 | - | Møhl and Anderson 1973 |
| | | click | - | 110-150 | 135-177 | Busnel *et al.* 1965; Møhl and Anderson 1973; Kamminga and Wiersma 1981; Akamatsu *et al.* 1994 |
| *Phocoena sinus* | Vaquita | click | - | 128-139 | - | Silber 1991 |
| Physeteridae | | | | | | |
| *Kogia breviceps* | Pygmy sperm whale | clicks | 60-200 | 120 | - | Santoro *et al.* 1989, Caldwell and Caldwell 1987 |
| *Physeter catadon* | Sperm whale | clicks | 0.1-30 | 2-4, 10-16 | 160-180 | Backus and Schevill 1966; Levenson 1974; Watkins 1980a |
| | | coda | 16-30 | - | - | Watkins 1980a |
| Platanistoidea | | | | | | |
| Iniidae | | | | | | |
| *Inia geoffrensis* | Boutu | squeals | <1-12 | 1-2 | - | Caldwell and Caldwell 1970 |
| | | whistle | 0.2-5.2 | 1.8-3.8[b] | - | Wang Ding *et al.* 1995 |
| | | click | 25-200 | 100 | - | Norris *et al.* 1972 |
| | | | | 95-105 | - | Kamminga *et al.* 1989 |
| | | click | - | 85-105 | - | Diercks *et al.* 1971; Evans 1973; Kamminga *et al.* 1993 |
| | | click | 20-120 | - | 156 | Xiao Youfu and Jing Rongcai 1989 |
| Platanistidae | | | | | | |

| | | | | | | |
|---|---|---|---|---|---|---|
| *Platanista minor* | Indus susu | clicks | 0.8-16 | - | low | Andersen and Pilleri 1970; Pilleri *et al.* 1971 |
| | | click | - | 15-100 | - | Herald *et al.* 1969 |
| Pontoporiidae | | | | | | |
| *Lipotes vexillifer* | Baiji | whistles | 3-18.4 | 6 | 156 | Jing Xianying *et al.* 1981; Xiao Youfu and Jing Rongcai 1989 |
| *Pontoporia blainvillei* | Franciscana | click | 0.3-24 | - | - | Busnel *et al.* 1974 |
| Ziphiidae | | | | | | |
| *Hyperoodon ampullatus* | Northern bottle-nose whale | whistles | 3-16 | - | - | Winn *et al.* 1970 |
| | | clicks | 0.5-26 | - | - | Winn *et al.* 1970 |
| *Hyperoodon spp.* | Bottlenose whale | click | - | 8-12 | - | Winn *et al.* 1970 |
| *Mesoplodon carlhubbsi* | Hubb's beaked whale | pulses | 0.3-80 | 0.3-2 | - | Buerki *et al.* 1989; Lynn and Reiss 1992 |
| *Mesoplodon densirostris* | Blainville's beaked whale | whistles, chirps | <1-6 | - | - | Caldwell and Caldwell 1971a |
| | | whistles | 2.6-10.7 | - | - | Buerki *et al.* 1989; Lynn and Reiss 1992 |
| Mysticeti | | | | | | |
| Balaenidae | | | | | | |
| *Balaena mysticetus* | Bowhead | calls | 0.100-0.580 | 0.14-0.16 | 128-190 | Thompson *et al.* 1979; Ljungblad *et al.* 1980; Norris and Leatherwood 1981; Würsig and Clark 1993 |
| | | tonal moans | 0.025-0.900 | 0.10-0.40 | 128-178 | Ljungblad *et al.* 1982; Cummings and Holliday 1987; Clark *et al.* 1986 |
| | | pulsive | 0.025-3.500 | - | 152-185 | Clark and Johnson 1984; Würsig *et al.* 1985; Cummings and Holliday 1987 |
| | | song | 0.02-0.50 | <4 | 158-189 | Ljungblad *et al.* 1982; Cummings and Holliday 1987; Würsig and Clark 1993 |
| *Eubalaena australis* | Southern right whale | tonal | 0.03-1.25 | 0.16-0.50 | - | Cummings *et al.* 1972; Clark 1982, 1983 |

| | | | | | | |
|---|---|---|---|---|---|---|
| | | pulsive | 0.03-2.20 | 0.05-0.50 | 172-187 | Cummings *et al.* 1972; Clark 1982, 1983 |
| | | | | | 181-186 | Clark (in Würsig *et al.* 1982) |
| *Eubalaena glacialis* | Northern right whale | call | <0.400 | <0.200 | - | Watkins and Schevill 1972; Clark 1990 |
| | | moans | <0.400 | - | - | Watkins and Schevill 1972; Thompson *et al.* 1979; Spero 1981 |
| Neobalaenidae | | | | | | |
| *Caperea marginata* | Pygmy right whale | thumps in pairs | <0.300 | 0.060-0.135 | 165-179 | Dawbin and Cato 1992 |
| Balaenopteridae | | | | | | |
| *Balaenoptera acutorostrata* | Minke whale | down sweeps | 0.06-0.13 | - | 165 | Schevill and Watkins 1972 |
| | | moans, grunts | 0.06-0.14 | 0.06-0.14 | 151-175 | Schevill and Watkins 1972; Winn and Perkins 1976 |
| | | ratchet | 0.85-6 | 0.85 | - | Winn and Perkins 1976 |
| | | thump trains | 0.10-2 | 0.10-0.20 | - | Winn and Perkins 1976 |
| *Balaenoptera borealis* | Sei whale | FM sweeps | 1.5-3.5 | - | - | Thompson *et al.* 1979; Knowlton *et al.* 1991 |
| *Balaenoptera edeni* | Bryde's whale | moans | 0.070-0.245 | 0.124-0.132 | 152-174 | Cummings *et al.* 1986 |
| | | pulsed moans | 0.10-0.93 | 0.165-0.900 | - | Edds *et al.* 1993 |
| | | discrete pulses | 0.70-0.95 | 0.700-0.900 | - | Edds *et al.* 1993 |
| *Balaenoptera musculus* | Blue whale | moans | 0.012-0.400 | 0.012-0.025 | 188 | Cummings and Thompson 1971, 1994; Edds 1982; Stafford *et al.* 1994 |
| *Balaenoptera physalus* | Fin whale | moans | 0.016-0.750 | 0.020 | 160-190 | Thompson *et al.* 1979; Edds 1988 |
| | | pulse | 0.040-0.075 | - | - | Clark 1990 |
| | | pulse | 0.018-0.025 | 0.020 | - | Watkins 1981 |
| | | ragged pulse | <0.030 | - | - | Watkins 1981 |
| | | rumble | - | <0.030 | - | Watkins 1981 |
| | | moans, downsweeps | 0.014-0.118 | 0.020 | 160-186 | Watkins 1981; Watkins *et al.* 1987; Edds 1988; Cummings and Thompson 1994 |
| | | constant call | 0.02-0.04 | - | - | Edds 1988 |
| | | moans, tones, upsweeps | 0.03-0.75 | - | 155-165 | Watkins 1981; Cummings *et al.* 1986; Edds 1988 |
| | | rumble | 0.01-0.03 | - | - | Watkins 1981; Edds 1988 |

| | | | | | | |
|---|---|---|---|---|---|---|
| | | whistles[e], chirps[e] | 1.5-5 | 1.5-2.5 | - | Thompson *et al.* 1979 |
| | | clicks[e] | 16-28 | - | - | Thompson *et al.* 1979 |
| *Megaptera novaeangliae* | Humpback whale | songs | 0.03-8 | 0.1-4 | 144-186- | Thompson *et al.* 1979;Watkins 1981; Edds 1982,1988; Payne *et al.* 1983; Silber 1986; Clark 1990 |
| | | social | 0.05-10 | <3 | - | Thompson *et al.* 1979 |
| | | song components | 0.03-8 | 0.120-4 | 144-174 | Thompson *et al.* 1979; Payne and Payne 1985 |
| | | shrieks | - | 0.750-1.8 | 179-181 | Thompson *et al.* 1986 |
| | | horn blasts | - | 0.410-0.420 | 181-185 | Thompson *et al.* 1986 |
| | | moans | 0.02-1.8 | 0.035-0.360 | 175 | Thompson *et al.* 1986 |
| | | grunts | 0.025-1.9 | - | 190 | Thompson *et al.* 1986 |
| | | pulse trains | 0.025-1.25 | 0.025-0.080 | 179-181 | Thompson *et al.* 1986 |
| | | slap | 0.03-1.2 | - | 183-192 | Thompson *et al.* 1986 |
| Eschrichtiidae | | | | | | |
| *Eschrictius robustus* | Gray whale | call | 0.2-2.5 | 1-1.5 | - | Dahlheim and Ljungblad 1990 |
| | | moans | 0.02-1.20 | 0.02-0.2, 0.7-1.2 | 185 | Cummings *et al.* 1968; Fish *et al.* 1974; Swartz and Cummings 1978 |
| | | modulated pulse | 0.08-1.8 | 0.225-0.600 | - | Dahlheim *et al.* 1984; Moore and Ljungblad 1984 |
| | | FM sweep | 0.10-0.35 | 0.300 | - | Dahlheim *et al.* 1984; Moore and Ljungblad 1984 |
| | | pulses | 0.10-2 | 0.300-0.825 | - | Dahlheim *et al.* 1984; Moore and Ljungblad 1984 |
| | | clicks (calves) | 0.10-20 | 3.4-4 | - | Fish *et al.* 1974; Norris *et al.* 1977 |
| Fissipedia | | | | | | |
| Mustelidae | | | | | | |
| Enhydra lutris | Sea otter | growls[c] whine | 3-5 | - | - | Kenyon 1981; Richardson *et al.* 1995 |
| Pinnipedia | | | | | | |
| Odobenidae | | | | | | |
| *Odobenus rosmarus* | Walrus | bell tone | - | 0.4-1.2 | - | Schevill *et al.* 1966; Ray and Watkins 1975; Stirling *et al.* 1983 |
| | | clicks,taps, knocks | 0.1-10 | <2 | - | Schevill *et al.* 1966; Ray and Watkins 1975; Stirling *et al.* 1983 |

| | | | | | | |
|---|---|---|---|---|---|---|
| | | rasps | 0.2-0.6 | 0.4-0.6 | - | Schevill *et al.* 1966 |
| | | grunts | ≤1 | ≤1 | - | Stirling *et al.* 1983 |
| Otariidae | | | | | | |
| *Arctocephalus philippii* | Juan Fernandez fur seal | clicks | 0.1-0.2 | 0.1-0.2 | - | Norris and Watkins 1971 |
| *Callorhinus ursinus* | Northern fur seal | clicks,bleats | - | - | - | Poulter 1968 |
| *Eumetopias jubatus* | Northern sea lion | clicks,growls | - | - | - | Poulter 1968 |
| *Zalophus californianus* | California sea lion | barks | <8 | <3.5 | - | Schusterman *et al.* 1967 |
| | | whinny | <1-3 | - | - | Schusterman *et al.* 1967 |
| | | clicks | - | 0.5-4 | - | Schusterman *et al.* 1967 |
| | | buzzing | <1-4 | <1 | - | Schusterman *et al.* 1967 |
| Phocidae | | | | | | |
| *Cystophora cristata* | Hooded seal | grunt | - | 0.2-0.4 | - | Terhune and Ronald 1973 |
| | | snort | - | 0.1-1 | - | Terhune and Ronald 1973 |
| | | buzz(click) | to 6 | 1.2 | - | Terhune and Ronald 1973 |
| *Erignathus barbatus* | Bearded seal | song | 0.02-6 | 1-2 | 178 | Ray *et al.* 1969; Stirling *et al.* 1983; Cummings *et al.* 1983 |
| *Halichoerus grypus* | Grey seal | clicks, hiss | 0-30, 0-40 | - | - | Schevill *et al.* 1963; Oliver 1978 |
| | | 6 call types | 0.1-5 | 0.1-3 | - | Asselin *et al.* 1993 |
| | | knocks | to 16 | to 10 | - | Asselin *et al.* 1993 |
| *Hydrurga leptonyx* | Leopard seal | pulses and trills | 0.1-5.9 | - | - | Ray 1970; Stirling and Siniff 1979; Rogers *et al.* 1995 |
| | | thump,blast | 0.04-7 | - | - | Rogers *et al.* 1995 |
| | | ultrasonic | up to 164 | 50-60 | low | Thomas *et al.* 1983a |
| *Leptonychotes weddellii* | Weddell seal | >34 call types | 0.1-12.8 | - | 153-193 | Thomas and Kuechle 1982; Thomas *et al.* 1983b; Thomas and Stirling 1983 |
| *Lobodon carcinophagus* | Crabeater seal | groan | <0. 1-8 | 0.1-1.5 | high | Stirling and Siniff 1979 |
| *Ommatophoca rossii* | Ross seal | pulses | 0.25-1 | - | - | Watkins and Ray 1985 |
| | | siren | 4-1-4 | - | - | Watkins and Ray 1985 |
| *Phoca fasciata* | Ribbon seal | frequency sweeps | 0.1-7.1 | - | 160 | Watkins and Ray 1977 |
| *Phoca (Pagophilus) groenlandica* | Harp seal | 15 sound types | <0.1-16 | 0.1-3 | 130-140 | Møhl *et al.* 1975; Watkins and Schevill 1979; Terhune and Ronald 1986; Terhune 1994 |

| | | | | | | |
|---|---|---|---|---|---|---|
| | | clicks | - | 30 | 131-164 | Møhl *et al.* 1975 |
| *Phoca hispida* | Ringed seal | barks, clicks, yelps | 0.4-16 | <5 | 95-130 | Stirling 1973; Cummings *et al.* 1984 |
| *Phoca largha* | Spotted seal | social sounds | 0.5-3.5 | - | - | Beier and Wartzok 1979 |
| *Phoca vitulina* | Harbor seal | clicks | 8-150 | 12-40 | - | Schevill *et al.* 1963; Cummings and Fish 1971; Renouf *et al.* 1980; Noseworthy *et al.* 1989 |
| | | roar | 0.4-4 | 0.4-0.8 | - | Hanggi and Schusterman 1992, 1994 |
| | | growl, grunt, groan | <0.1-0.4 | <0.1-0.25 | - | Hanggi and Schusterman 1992, 1994 |
| | | creak | 0.7-4 | 0.7-2 | - | Hanggi and Schusterman 1992, 1994 |
| Sirenia | | | | | | |
| Dugongidae | | | | | | |
| *Dugong dugon* | Dugong | chirp-squeak[c] | 3-8 | - | low | Nair and Lal Mohan 1975 |
| | | sound 1[c] | 1-2 | - | | Marsh *et al.* 1978 |
| | | chirp[c] | 2-4 | - | - | Marsh *et al.* 1978 |
| | | all sounds | 0.5-18 | 1-8 | | Nishiwaki and Marsh 1985; Anderson and Barclay 1995 |
| Trichechidae | | | | | | |
| *Trichechus inunguis* | Amazon manatee | squeaks,pulses | 6-16 | 6-16 | - | Evans and Herald 1970 |
| *Trichechus manatus* | West Indian manatee | squeaks | 0.6-16 | 0.6-5 | low | Schevill and Watkins 1965 |

[a]Equipment capable of recording to 10 kHz only.

[b]Frequency determined as "mean minimum frequency minus 1 s.d...to...mean maximum frequency plus 1 s.d." (*sensu* Richardson *et al* 1995).

[c]Recorded in air.

[d]Performance in high background noise (Au, 1993)

[e] Few recordings or uncertain verification of sound for species.

**NOAA Technical Memorandum NMFS**

This TM series is used for documentation and timely communication of preliminary results, interim reports, or special purpose information. The TMs have not received complete formal review, editorial control, or detailed editing.

**SEPTEMBER 1998**

# MARINE MAMMAL AUDITORY SYSTEMS: A SUMMARY OF AUDIOMETRIC AND ANATOMICAL DATA AND ITS IMPLICATIONS FOR UNDERWATER ACOUSTIC IMPACTS

Darlene R. Ketten, Ph. D.

Associate Scientist
Department of Biology
Woods Hole Oceanography Institution
and
Assistant Professor
Department of Otology and Laryngology
Harvard Medical School

in accordance with order number
40JGNF600312 issued 8/27/96
NOAA, National Marine Fisheries Service
La Jolla, California 92038-0271

NOAA-TM-NMFS-SWFSC-256

**U.S. DEPARTMENT OF COMMERCE**
William M. Daley, Secretary

**National Oceanic and Atmospheric Administration**
D. James Baker, Under Secretary for Oceans and Atmosphere

**National Marine Fisheries Service**
Rolland A. Schmitten, Assistant Administrator for Fisheries

## Explanatory Note

This report is one in a series on the potential for technology applications to enhance efficiency in commercial fisheries, reduce the catch of non-targeted species, and provide new tools for fishery assessments in support of the NMFS strategic goals to build sustainable fisheries and recover protected species. We hope the distribution of this report will facilitate further discussion and research into the application's potential usefulness, but should not be construed as an endorsement of the application by NMFS.

Pursuant to changes in the Marine Mammal Protection Act in 1988, the NMFS' SWFSC began another series of ETP-related studies in 1990, focused on developing and evaluating methods of capturing yellowfin tuna which do not involve dolphins. This series of studies has been conducted within the SWFSC's Dolphin-Safe Research Program. Studies on the potential use of airborne lidar (LIght Detection And Ranging) systems began in 1991, and studies on low-frequency acoustic systems to detect fish schools at ranges much greater than currently possible were initiated during 1995. In addition to their use as an alternative to fishing on dolphins, these systems have potential to increase the efficiency of the fishing operations by locating fish schools not detectable by customary visual means, and as a fishery-independent tool to conduct population assessments on pelagic fish. They also have potential to adversely impact marine animals.

The Dolphin-Safe Research Program is investigating, through a series of contracts and grants, five airborne lidars: 1) the NMFS-developed "Osprey" lidar (Oliver et al. 1994), 2) the Kaman Aerospace Corporation's FISHEYE imaging lidar (Oliver and Edwards 1996), 3) the NOAA Environmental Technology Laboratory's Experimental Oceanographic Fisheries Lidar (Churnside et al. 1998), 4) the Arete Associates 3D Streak-Tube Imaging Lidar, and 5) the Detection Limited's lidar . An initial study on the potential effects of airborne lidars on marine mammals will be completed during 1998 (Zorn et al. 1998).

The Dolphin-Safe Research Program has completed, through a series of contracts and grants, acoustic system studies on 1) the acoustic target strength of large yellowfin tuna schools (Nero 1996), 2) acoustic detection parameters and potential in the eastern tropical Pacific Ocean (Rees 1996), 3) the design of two towed acoustic systems (Rees 1998, Denny et al. 1998), 4) measurements of swimbladder volumes from large yellowfin tuna (Schaefer and Oliver 1998) and, 5) **the potential effects of low-frequency sound on marine mammals (Ketten 1998)**.

Chuck Oliver
Dolphin-Safe Research Program
Southwest Fisheries Science Center
P.O. Box 271
La Jolla, California 92037

## Dolphin-Safe Research Program Detection Technology Reports


Churnside, J.H., J.J. Wilson, and C.W. Oliver. 1998. Evaluation of the capability of the experimental oceanographic fisheries lidar (FLOE) for tuna detection in the eastern tropical Pacific. Environmental Technology Laboratory, Boulder, CO.

Denny, G.F., K.E. deVilleroy, and P.K. Simpson. 1998. Long-range tuna school detection sonar system design specification. Grant (NA77FD0044) report. Scientific Fishery Systems, Inc., Anchorage, AK., 38 p.

**Ketten, D. 1998. Marine mammal auditory systems: a summary of audiometric and anatomical data and its implications for underwater acoustic impacts. Contract (40JBNF600312) report. Boston, MA.**

Nero, R. W. 1996. Model estimates of acoustic scattering from schools of large yellowfin tuna. Contract (40ABNF510351) report NRL/MR/774-95-7708. Naval Research Lab. Stennis Space Center, MS. 21p

Oliver, C., W. Armstrong, and J. Young 1994. "Development of an airborne LIDAR system to detect tunas in the eastern tropical Pacific purse-seine fishery" NOAA-TM-NMFS-SWFSC-204. 65 p.

Oliver, C.W. and Edwards, E.F. 1996. Dolphin-Safe Research Program Progress Report II (1992-1996). Southwest Fisheries Science Center Admin. Rpt. LJ-96-13. 91p.

Rees, C. D. 1996. Modeling of acoustic detection of yellowfin tuna in the eastern tropical Pacific fishery area. Contract (40ABNF510351) report. NCCOSC Code 541, San Diego, CA. 83p plus appendices.

Rees, C. D. 1998. Active towed-array acoustic system design study for yellowfin tuna in the eastern tropical Pacific fishery area. Contract (43ABNF61572) report. NCCOSC Code 541, San Diego, CA. 58p plus appendices

Schaefer, K. M. and C. W. Oliver. (in review). Shape, volume, and resonance frequency of the swimbladder of yellowfin tuna (*Thunnus albacares*). Contract (40JGNF700270) report. Inter-American Tropical Tuna Commission, La Jolla, CA.

Zorn, H.M., J.H. Churnside, and C.W. Oliver. 1998 (in review). Laser safety thresholds for cetaceans and pinnipeds. Environmental Technology Laboratory, Boulder, CO.

**Table of Contents**

## Table of Contents

## List of Tables

## List of Figures

## List of Figures

## Acknowledgments

Production of this report was supported through contract no. 40JGNF600312, awarded by NOAA, National Marine Fisheries Service, La Jolla, California. Segments of the report were excerpted from previous publications by the author. Original data from the author's research related to acoustic trauma were obtained through support from the Office of Naval Research and National Institutes of Health, Deafness and Communication Disorders. The author is very grateful to the reviewers for their comments. Suggestions from Charles Oliver and Roger Gentry were particularly helpful in improving the clarity and relevance of this document.

# A SUMMARY OF AUDIOMETRIC AND ANATOMICAL DATA AND ITS IMPLICATIONS FOR UNDERWATER ACOUSTIC IMPACTS

Darlene R. Ketten, Ph. D.

Associate Scientist
Department of Biology
Woods Hole Oceanographic Institution

Assistant Professor
Dept. of Otology and Laryngology
Harvard Medical School

## Abstract

This report summarizes and critiques existing auditory data for marine mammals. It was compiled primarily as a background or reference document for assessing probable impacts of long-range detection devices that may be employed in tuna fisheries. To that end, it has the following emphases: a description of currently available data on marine mammal hearing and ear anatomy, a discussion and critique of the methods used to obtain these data, a summary and critique of data based on hearing models for untested marine species, and a discussion of data available on acoustic parameters that induce auditory trauma in both marine and land mammals. In order to place these data in an appropriate context, summaries are incorporated also of basic concepts involved in underwater vs. air-borne sound propagation, fundamental hearing mechanisms, and mechanisms of auditory trauma in land mammals.

Although the primary purpose of this report is to provide a reference document on the state of knowledge of marine mammal hearing, it is expected that the material will be used as a resource for assisting with the design and assessment of the safety and efficacy of acoustic detection and censusing devices used in fisheries, particularly for the Eastern Tropical Pacific region. Consequently, to maximize the utility of this document, a brief discussion has been included on the potential for impact on hearing from several recently proposed devices and an outline of research areas that need to be addressed if we are to fill the relatively large gaps in the existing data base.

The data show that marine mammals have a fundamentally mammalian ear that through adaptation to the marine environment has developed broader hearing ranges than those common to land mammals. Audiograms are available for 11 species of odontocetes and pinnipeds. For most marine mammal species, we do not have direct behavioral or physiologic audiometric data. For those species for which audiograms are not available, hearing ranges can be estimated with mathematical models based on ear anatomy or inferred from emitted sounds and play back experiments. The combined data show there is considerable variation among marine mammals in both absolute hearing range and sensitivity, and the composite range is from ultra to infrasonic. Odontocetes, like bats, are excellent echolocators, capable of producing, perceiving, and analyzing ultrasonics frequencies (defined as >20 kHz). Odontocetes commonly have good functional hearing between 200 Hz and 100 kHz, although individual species may have functional ultrasonic hearing to nearly 200 kHz. The majority of odontocetes have peak sensitivities in the ultrasonic ranges although most have moderate sensitivity from 1 to 20 kHz. No odontocete has been shown audiometrically to have acute hearing (<80 dB re 1 μPa) below 500 Hz.

Good lower frequency hearing is confined to larger species in both the cetaceans and pinnipeds. No mysticete has been directly tested for any hearing ability, but functional models indicate that their functional hearing range commonly extends to 20 Hz, with several species

expected to hear well into infrasonic frequencies. The upper functional range for most mysticetes has been predicted to extend to 20-30 kHz.

Most pinniped species have peak sensitivities from 1-20 kHz. Some species, like the harbour seal, have best sensitivities over 10 kHz; only the elephant seal has been shown to have good to moderate hearing below 1 kHz. Some pinniped species are considered to be effectively double-eared in that they hear moderately well in two domains, air and water, but are not particularly acute in either. Others however are clearly best adapted for underwater hearing alone.

To summarize, marine mammals as a group have functional hearing ranges of 10 Hz to 200 kHz with best thresholds near 40 dB re 1 μPa. They can be divided into infrasonic balaenids (probable functional ranges of 15 Hz to 20 kHz; good sensitivity from 20 Hz to 2 kHz; threshold minima unknown, speculated to be 80 dB re 1 μPa); sonic to high frequency species (100 Hz to 100 kHz; widely variable peak spectra; minimal threshold commonly 50 dB re 1 μPa), and ultrasonic dominant species (500 Hz to 200 kHz general sensitivity; peak spectra 16 kHz to 120 kHz; minimal threshold commonly 40 dB re 1 μPa).

The consensus of the data is that virtually all marine mammal species are potentially impacted by sound sources with a frequency of 500 HZ or higher. Relatively few species are likely to receive significant impact for lower frequency sources. Those that are likely candidates for LFS impact are all mysticetes and the elephant seal. By contrast, most pinnipeds have relatively good sensitivity in the 1-15 kHz range while odontocetes have peak sensitivities above 20 kHz. These "typical" ranges are generalities based on the mode of the data available for each group. It must be remembered that received levels that induce acoustic trauma, at any one frequency, are highly species dependent and are a complex interaction of exposure time, signal onset and spectral characteristics, and received vs. threshold intensity for that species at that frequency. Pilot studies show that marine mammals are susceptible to hearing damage but are not necessarily as fragile as land mammals. The available data suggest that a received level of 80 to 140 dB over species-specific threshold for a narrow band source will induce temporary to permanent loss for hearing in and near that band in pinnipeds and delphinids (Ridgway, pers. comm.; Schusterman, pers. comm.). Estimates of levels that induce temporary threshold shift in marine mammals can be made, at this time, only by extrapolation from trauma studies in land mammals. By comparison, because of mechanistic differences, blasts or rapid onset sources are capable of inducing broad hearing losses in virtually all species. Incidence of damage from blasts that results from middle ear air volume effects is speculated to be, to some extent, animal mass dependent rather than auditorially dependent.

For all devices, given that impulsive noise can be avoided, the question of impact devolves largely to the coincidence of device signal characteristics with the species audiogram. Because the majority of devices proposed use frequencies below ultra or high sonic ranges, odontocetes, with relatively poor sensitivity below 1 kHz as a group, may be the least likely animals to be impacted. Mysticetes and pinnipeds have substantially greater potential than odontocetes for direct acoustic impact because of better low to mid-sonic range hearing. Behavioral perturbations are not assessed in the report, but a concern is noted that they may be equally or more important as acoustic impacts. Mitigation, like estimation of impact, requires a case by case assessment, and therefore suffers from the same lack of data. To provide adequate estimates for both, substantially better audiometric data are required from more species. To obtain these data requires an initial three-pronged effort of behavioural audiograms, evoked potentials recordings, and post-mortem examination of ears across a broad spectrum of species. Cross-comparisons of the results of these efforts will provide a substantially enhanced audiometric data base and should provide sufficient data to predict all levels of impact for most marine mammals.

## Introduction

Since the development and use of SONAR in World War II, acoustic imaging devices have been increasingly employed by the military, research, and commercial sectors to obtain reliable, detailed information about the oceans. On one hand, these devices have enormous potential for imaging and monitoring the marine environment. On the other hand, because echo-ranging techniques involve the use of intense sound and because hearing is an important sensory channel for virtually all marine vertebrates, existing devices also represent a potential source of injury to marine stocks. Therefore, a reasonable concern for any effort involving active sound use in the oceans is whether the projection and repetition of the signals employed will adversely impact species within the "acoustic reach" of the source. Realistically, because of the diversity of hearing characteristics among marine animals, it is virtually impossible to eliminate all acoustic impacts from any endeavor, therefore the key issues that must be assessed are: 1) what combination of frequencies and sound pressure levels fit the task, 2) what species are present in an area the device will ensonify at levels exceeding ambient, and 3) what are the potential impacts to those species from acoustic exposures to the anticipated frequency-intensity combinations.

In order to assess potential impacts, it is necessary to obtain the best possible estimate of the coincidence of acoustic device parameters and auditory sensitivities for animals that may be exposed. Because marine mammals are both an important group in terms of conservation and are generally considered to be acoustically sensitive, the primary goal of this document is to provide a detailed summary of currently available data on marine mammal hearing and auditory systems, and where possible to put that data into a functional or comparative context. The key issues addressed are: 1) how do marine mammal ears differ from terrestrial ears, 2) how do these differences correlate with underwater sound perception, 3) what is known from direct measures about marine mammal hearing sensitivities, 4) what can be reliably extrapolated about the frequency sensitivity of untested species from currently available auditory models, and 5) how sensitive to acoustic impacts are these ears.

## Sensory System Concepts: Do Marine Mammals Fit the Pattern?

The term "auditory system" refers generally to the peripheral components an animal uses to detect and analyze sound. There are two fundamental issues to bear in mind for the auditory as well as any sensory system. One is that sensory systems and therefore perception are species-specific. The second is that they are habitat dependent. In terms of hearing, both of these are important issues.

Concerning the first issue, species sensitivities, all sensory systems are designed to allow animals to receive and process information from their surroundings. The sensory systems of marine mammals are similar to those of terrestrial mammals in that they act as highly selective filters. If every environmental cue available received equal attention, the brain would be barraged by sensory inputs. Instead, sensory organs are essentially multi-level filters, selecting and attending to signals that, evolutionarily, proved to be important.

Most animals have vocalizations that are tightly linked to their peak hearing sensitivities in order to maximize intra-specific communication, but they also have hearing beyond that peak range that is related to the detection of acoustic cues from predators, prey, or other significant environmental cues. Consider, in general, how predator and prey are driven to be both similar and different sensorially. Because their activities intersect in place and time, they need, for example, to have similar visual and auditory sensitivities, but, ideally, different fields of view and hearing ranges. Similarly, two species living within similar habitats or having common predators and prey have some hearing bands in common but will differ in total range because of anatomical and functional differences that are species dependent and reflect other "species-specific" needs. Thus, each animal's perceived world is a different subset of the real physical world; *i.e.*, it is a species-specific model, constructed from the blocks of data its particular sensory system can capture and process. Two species may have overlapping hearing ranges, but no two have identical sensitivities. This is of course the case with piscivorous marine mammals, their fish targets, and with their prey competitors. For the primary concern in this document, placing the marine mammal ear in the context of impact by fish detection devices, this is a particularly cogent point.

In animal behavior, this concept is called the Umwelt (von Uexküll 1934). As a technical term, Umwelt means an animal's perceptually limited construct of the world. In common usage, it means simply the environment. This dual meaning reflects the complex interaction of sensory adaptations and habitat, which leads us to the second issue; i.e., the relation or influence of habitat on sensory abilities. While senses are tuned to relevant stimuli by evolution they are nevertheless limited by the physical parameters of the habitat.

For example, human sensory systems are geared to diurnal, air-borne cues. Humans are highly developed visually, with 38 times more optic nerve fibers than auditory nerve fibers, but our hearing range (20 to 20,000 Hz, or 8 octaves) is relatively narrow compared to many other mammals. In part, this is because diurnal land mammals have visual cues that are generally more abundant and specific than acoustic cues. By contrast, nocturnal species are generally better developed auditorially than visually, relying on hearing rather than vision in a dim environment.

**Hearing Fundamentals**

The adaptive importance of sound cues is underscored by the ubiquity of hearing. There are lightless habitats on earth with naturally blind animals, but no terrestrial habitat is without sound, and no known vertebrate, with the possible exception of agnathans, that is naturally profoundly deaf. Mechanistically, hearing is a relatively simple chain of events: sound energy is converted by bio-mechanical transducers (middle and inner ear) into electrical signals (neural impulses) that provide a central processor (brain) with acoustic data. Mammalian ears are elegant structures, packing over 75,000 mechanical and electrochemical components into an average volume of 1 $cm^3$. Variations in the structure and number of ear components account for most of the hearing capacity differences among mammals (see Webster *et al.* 1992 for an overview).

Hearing ranges and the sensitivity at each audible frequency (threshold, or minimum intensity required to hear a given frequency) vary widely by species (Figure 1). "Functional" hearing refers to the range of frequencies a species hears without entraining non-acoustic mechanisms. In land mammals, the functional range is generally considered to be those frequencies that can be heard at thresholds of 60 dB SPL, a decibel measure of sound pressure level. The basis for this measure and how it differs in air and water are explained in detail in the next section. By example, a healthy human ear has a potential maximum frequency range of 0.02 to 20 kHz but the normal functional hearing range in an adult is closer to 0.040 to 16 kHz (Fig. 2). In humans, best sensitivity (lowest thresholds) occurs between 500 Hz and 4 kHz, which is also where most acoustic energy of speech occurs (Schuknecht 1993, Yost 1994). Sounds that are within the functional range but at high intensities (beyond 120 dB SPL) will generally produce discomfort and eventually pain. To hear frequencies at the extreme ends of any animal's total range generally requires intensities that are uncomfortable, and frequencies outside or beyond our hearing range are simply undetectable because of limitations in the ear's middle and inner ear transduction and resonance characteristics. Through bone conduction or direct motion of the inner ear, exceptionally loud sounds that are outside the functional range of the normal ear can sometimes be perceived, but this is not truly an auditory sensation.

"Sonic" is an arbitrary term derived from the maximal human hearing range. Frequencies outside this range are deemed infrasonic (below 20 Hz) or ultrasonic (above 20 kHz) sonic. By observation, we know that many animals hear sounds inaudible to humans. Most mammals have some ultrasonic hearing (i.e., can hear well at frequencies >20 kHz) and a few, like the Asian elephant, *Elephas maximus*, hear infrasonic signals (<20 Hz).

Hearing ranges are both animal size and niche related. In general, mammalian ears scale with body size (Manley 1972; Ketten 1984, 1992; West 1986). The highest frequency an animal hears is generally inversely related to body mass; smaller animals typically have good high frequency hearing while larger animals tend to have lower overall ranges (von Békesy 1960, Greenwood 1962, Manley 1972, Ketten 1984, West 1986), but, regardless of size, crepuscular and nocturnal species typically have acute ultrasonic hearing while subterranean species usually have good infrasonic hearing, and, in some cases, can detect seismic vibrations (Sales and Pye 1974, Heffner and Heffner 1980, Payne *et al.* 1986, Fay 1988).

How well do marine mammals mesh with this general land mammal hearing scheme? As noted above, similar sensitivities are to be expected among species that have similar adaptation pressures. These are essentially terrestrial ears immersed in a biologically rich but harsh environment. Anatomically, they follow the basic land mammal pattern but they have extensive adaptations that accommodate substantial parasite loads, pressure changes, and concussive forces. On one hand, having ears that are basically similar to other mammals implies they are subject to conventional, progressive auditory debilitation. Relatively noisy oceanic environments could aggravate this problem. On the other hand, because marine mammals evolved in a high noise environment and have adaptations that prevent inner ear damage from barotrauma, it is possible they are less susceptible to noise and age-related loss.

Marine mammals evolved from land-dwelling ancestors during the explosive period of mammalian radiation (see Barnes *et al.* 1985), and they retained the essentials of air-adapted ears; *e.g.*, an air-filled middle ear and spiral cochlea. Therefore, some similarities in hearing mechanisms are not surprising. Today, marine mammals occupy virtually every aquatic niche (fresh water to pelagic, surface to profundal) and have a size range of several magnitudes (*e.g.*, harbor porpoise, *Phocoena phocoena*: 1 m., 55 kg. vs. the blue whale, *Balaenoptera musculus*: 40 m., 94,000 kg.; Nowak 1991). We expect to see a wide range of hearing given their diversity of animal size and habitat. In fact, hearing in marine mammals has the same basic size vs. auditory structure relationship as in land mammals, but marine mammals have a significantly different auditory *bauplan*, or ear size vs frequency relationship (Solntseva 1971, 1990; Ketten 1984, 1992). Consequently, while some marine mammals, consistent with their size, hear well at low frequencies, the majority, despite their relatively large size, fit the nocturnal mammal pattern best and hear ultrasonic frequencies because of unique auditory mechanisms.

Land and marine ears have significant structural differences. Because of some of these differences, a common definition of the term "ear" is somewhat problematic. In this overview, ear is used in the broadest sense to encompass all structures that function primarily to collect and process sound. As marine mammal ancestors became more aquatic, air-adapted mammalian ears had to be coupled to water-borne sound for hearing to remain functional. Ear evolution took place in tandem with, and in part in response to, body reconfigurations. Just as the physical demands of operating in water exacted a structural price in the locomotory and thermoregulatory systems of marine mammals, physical differences in underwater sound required auditory system remodeling. In modern marine mammals, the extent of ear modifications parallels the level of aquatic adaptation in each group (Ketten 1984, 1992; Solntseva 1990). The greatest differences from land mammals are found in cetaceans and sirenians. As they evolved into obligate aquatic mammals, unable to move, reproduce, or feed on land, every portion of the head, including the auditory periphery was modified. As the rostrum elongated, the cranial vault foreshortened, and the nares and narial passages were pulled rearward to a dorsal position behind the eyes. Many land mammal auditory components, like external pinnae and air-filled external canals were lost or reduced and the middle and inner ears migrated outward. In most odontocetes, the ears have no substantial bony association with the skull. Instead, they are suspended by ligaments in a foam-filled cavity outside the skull (see anatomy section for detail). Consequently, they are effectively acoustically isolated from bone conduction, which is important for echolocation. There are also no bony, thin-walled air chambers, which is important for avoiding pressure related injuries. Specialized fatty tissues (low impedance channels for underwater sound reception) evolved that appear to function *in lieu* of external air-filled canals. Mysticete ears are as specialized but they appear to have been shaped more by size-related adaptations than by ultrasonic hearing and echolocation. Sirenian ears are not as well understood, but they appear to have many similar, highly derived adaptations. Today, cetacean and sirenian ears are so specialized for water-borne sound perception that they may no longer be able to detect or interpret air-borne sound at normal ambient levels. On the other hand, ears of sea otters and some otariids have very few anatomical differences from those of terrestrial mammals, and it is possible these ears represent a kind of amphibious compromise or even that they continue to be primarily air-adapted.

That brings us to three major auditory questions: 1) what are the differences between marine and terrestrial ears, 2) how do these differences relate to underwater hearing, and 3) how do these differences affect the acoustic impacts? To address these questions requires assimilating a wide variety of data. Behavioral and electrophysiological measures are available for some odontocetes and pinnipeds, but there are no published hearing curves for any mysticete, sirenian, or marine fissiped. Anatomical correlates of hearing are fairly well established (Manley 1972; Greenwood 1961, 1962, 1990; for reviews see Fay 1988, 1992; Echteler *et al.* 1994), and we have anatomical data on the auditory system for approximately one-third of all marine mammal species, including nearly half of the larger, non-captive species. Therefore, to give the broadest view of current marine mammal hearing data, both audiometric and anatomical data will be discussed. An outline of physical measures of sound in air vs. water and of the basic mechanisms of mammalian hearing are given first as background for these discussions.

## Sound in air vs. water

In analyzing marine mammal hearing, it is important to consider how the physical aspects of sound in air vs. water affect acoustic cues. Hearing is simply the detection of sound. "Sound" is the propagation of a mechanical disturbance through a medium. In elastic media like air and water, that disturbance takes the form of acoustic waves. Basic measures of sound are frequency, speed, wavelength, and intensity. Frequency, measured in cycles/sec or Hertz (Hz), is defined as:

$$f = c / \lambda \qquad (1)$$

where c = the speed of sound (m/sec) and is the wavelength (m/cycle). The speed of sound is directly related to the density of the medium. Because water is denser than air, sound in water travels faster and with less attenuation than sound in air. Sound speed in moist ambient surface air is approximately 340 m/sec. Sound speed in sea water averages 1530 m/sec but will vary with any factor affecting density. The principal physical factors affecting density in sea water are salinity, temperature, and pressure. For each 1% increase in salinity, speed increases 1.5 m/sec.; for each $1^{o}$ C decrease in temperature, 4 m/sec; and for each 100 m depth, 1.8 m/sec

(Ingmanson and Wallace 1973). Because these factors act synergistically, any ocean region can have a highly variable sound profile that may change both seasonally and regionally. For practical purposes, in water sound speed is 4.5 times faster and, at each frequency, the wavelength is 4.5 times greater, than in air.

How do these physical differences affect hearing? Mammalian ears are primarily sound intensity detectors. Intensity, like frequency, depends on sound speed and, in turn, on density. Sound intensity (I) is the acoustic power (P) impinging on a surface perpendicular to the direction of sound propagation, or power/unit area (I=P/a). In general terms, power is force times velocity (P=Fv). Pressure is force/unit area (p=F/a). Therefore, intensity can be rewritten as the product of sound pressure (p) and vibration velocity (v):

$$I = P / a = Fv / a = pv \quad (2)$$

For a traveling spherical wave, the velocity component becomes particle velocity (u), which can be defined in terms of effective sound pressure (p) the speed of sound in that medium (c), and the density of the medium ($\rho$):

$$u(x,t) = p / \rho c \quad (3)$$

We can then redefine intensity (2) for an instantaneous sound pressure for an outward traveling plane wave in terms of pressure, sound speed, and density (3):

$$I = pv = p(p / \rho c) = p^2 / \rho c \quad (4)$$

The product $\rho c$ is the characteristic impedance of the medium. Recalling that for air c=340 m/sec and for sea water c=1530 m/sec; for air, $\rho$=0.0013 g/cc; for sea water, $\rho$=1.03 g/cc, the following calculations using the intensity-pressure-impedance relation expressed in (4) show how physical properties of water vs. air influence intensity and acoustic pressure values:

$$I_{air} = p^2/(340\text{m/sec})(0.0013\text{ g/cc}) = p^2/(0.442\text{ g-m/sec-cc})$$
$$I_{water} = p^2/(1530\text{m/sec})(1.03\text{ g/cc}) = p^2/(1575\text{ g-m/sec-cc})$$

To examine the sensory implications of these equations, consider a hypothetical mammal, that hears equally well in water and in air. For this to be true, an animal with an intensity based ear would require the same acoustic power/unit area in water as in air to have an equal sound percept, or ($I_{air} = I_{water}$):

$$I_{air} = p_{air}^2/(0.442\text{ g-m/sec-cc}) = p_{water}^2/(1575.\text{g-m/sec-cc}) = I_{water}$$
$$p_{air}^2(3565.4) = p_{water}^2 \quad (5)$$
$$p_{air}(59.7) = p_{water}$$

This implies the sound pressure in water must be ~60 times that required in air to produce the same intensity and therefore the same sensation in the ear.

For technological reasons, received intensity, which is measured in watts/$m^2$, is difficult to determine. Consequently, we capitalize on the fact that intensity is related to the mean square pressure of the sound wave over time (4) and use an indirect measure, effective sound pressure level (SPL), to describe hearing thresholds (see Au 1993 for discussion). Sound pressure levels are conventionally expressed in decibels (dB), defined as:

$$\text{dB SPL} = 10 \log (p_m^2/p_r^2) \quad (6)$$
$$= 20 \log (p_m/p_r)$$

where $p_m$ is the pressure measured and $p_r$ is an arbitrary reference pressure. Currently, two standardized reference pressures are used. For air-borne sound measures, the reference is dB SPL or dB re 20 μPa rms, derived from human hearing. For underwater sound measures, the reference pressure is dB re 1 μPa.

Notice that decibels are a logarithmic scale based on a ratio that depends on reference pressure. In the earlier hypothetical example, with identical reference pressures, the animal needed a sound level ~35.5 dB greater in water than in air (from equation 5, 10 log 3565.4) to hear equally well. However, if conventional references for measuring levels in air vs. water are used, the differences in reference pressure must be considered as well. This means to produce an equivalent sensation in a submerged neffin, the underwater sound pressure level in water would need to be 35.5 dB + 20 (log 20) dB greater than the airborne value. That is, a sound level of 61.5 dB re 1 μPa in water is equivalent to 0 dB re 20 μPa in air. To the dual-eared or truly amphibious animal, they should sound the same because the intensities are equivalent. Thus, underwater sound intensities must be reduced by ~61.5 dB to be comparable numerically to intensity levels in air.

It is important to remember that these equations describe idealized comparison of air and water borne sound. In comparing data from different species, particularly in comparing terrestrial and marine mammal hearing data, experimental condition differences are extremely important. We have no underwater equivalent of anechoic chambers, often results are obtained from few individuals, and test conditions are highly variable.

## Marine Mammal Acoustics

## Sound Production

Recordings of naturally produced sounds are available for most marine mammal species (Watkins and Wartzok 1985), and they provide the broadest acoustic framework for hearing comparisons in species for which we have no audiometric data. Because mammalian vocalizations typically have peak spectra at or near the best frequency for that species, they are generally good indirect indicators of frequencies the animal normally hears well (Sales and Pye 1974, Popper 1980, Watkins and Wartzok 1985, Ketten and Wartzok 1990, Henson *et al.* 1990, Popov and Supin 1990a). A classic example is the discovery of ultrasonic signal use by dolphins (Kellogg 1959; Norris *et al.* 1961) which prompted several decades of investigations into echolocation and ultrasonic hearing abilities in marine mammals. However, it is also important to recall that sound production data obtained in a wide variety of background noise conditions cannot be used to infer minimal hearing thresholds because it is likely that produced sound levels are in some cases substantially louder than minimum audible levels in order to override background noise. For example, some recordings of odontocete and mysticete sounds have source levels estimated to be as high as 180 to 230 dB re 1 μPa (Richardson *et al.* 1991, Würsig and Clark 1993, Au 1993). For this document, their intended use is limited to being estimators of sound use categories or gross spectral differences among marine mammals.

*Cetaceans*

Cetaceans divide into high and low frequency sound producers that coincide with the two suborders (Table 1). Sound production data for odontocetes are consistent with the audiometric data; *i.e.*, ultrasonic use is common and differences in peak spectra of produced sounds are consistent with best frequency of hearing in species that have been tested (compare Table 1 and Figure 3). Mysticete sound production data imply they are primarily low frequency animals, and it is likely that many baleen species hear well at infrasonic frequencies.

Odontocetes produce species-stereotypic broadband clicks with peak energy between 10-200 kHz, individually variable burst pulse click trains, and constant frequency (CF) or frequency modulated (FM) whistles ranging from 4 to 16 kHz. Ultrasonic signals are highly species-specific and have been recorded from 21 species, although echolocation (or "biosonar") has been demonstrated in only 11 species of smaller odontocetes (Au 1993). All modern odontocetes are assumed, like bats, to be true echolocators, not simply ultrasonic receptors; *i.e.*, they "image" their environment by analyzing echoes from a self-generated ultrasonic signal (Kellogg 1959, Norris *et al.* 1961, Popper 1980, Wood and Evans 1980, Pilleri 1983, Watkins and Wartzok 1985). Echolocation is a two-way function; *i.e.*, to be an effective echolocator, an animal must have a coordinated means of generating a highly directional signal and receiving its echo. For this reason, evidence for high frequency ears alone is not sufficient to determine whether any marine mammal (or fossil species) is an echolocator.

Odontocetes vary pulse repetition rate, interpulse interval, intensity, and click spectra, particularly in response to high ambient noise (Schevill 1964, Norris 1969, Au *et al.* 1974, Popper 1980, Thomas *et al.* 1988, Moore 1990, Popov and Supin 1990a). Normally, however, each species has a characteristic echolocation frequency spectrum (Schevill 1964, Norris 1969, Popper 1980). Documented peak spectra of odontocete sonar signals range from 12 to 20 kHz (killer whale, *Orcinus orca*) to 120-140 kHz (*P. phocoena*) with source levels of 120-230 dB (Table 1).

The functional significance of species differences in the spectra of natural echolocation signals has not been directly tested, but there are strong correlations between habitat types and peak spectra (Gaskin 1976; Wood and Evans 1980; Ketten 1984). Considering that frequency and wavelength are inversely related, there is also an inverse relationship between frequency and the size of the object or detail that can be detected with echolocation. Based on their ultrasonic signals, odontocetes fall into two acoustic groups: Type I, with peak spectra (frequencies at maximum energy) above 100 kHz, and Type II, with peak spectra below 80 kHz (Ketten 1984, Ketten and Wartzok 1990) (Table 1). Type I echolocators are inshore and riverine dolphins that operate in acoustically complex waters. Amazonian Boutu, *Inia geoffrensis*, routinely hunt small fish amidst the roots and stems in silted, seasonal lakes and produce signals up to 200 kHz (Norris *et al.* 1972). *P. phocoena* typically use 110-140 kHz signals (Kamminga 1988). Communication signals are rare (or are rarely observed) in most Type I species (Watkins and Wartzok 1985); their auditory systems are characterized primarily by ultra-high-frequency adaptations consistent with short wavelength signals. Type II species are near- and off-shore animals (e.g., *Stenella*) that inhabit low object density environments, commonly travel in large pods, and, acoustically, are concerned with both communication with conspecifics and detection of relatively large, distant objects. They employ lower ultrasonic frequencies (40-70 kHz) with longer wavelengths that are consistent with detecting larger objects over greater distances and devote more acoustic effort to communication signals than Type I species.

Use of deep ocean stationary arrays has substantially increased our data base of mysticete sounds, and recent analyses suggest mysticetes have multiple, distinct sound production groups, but habitat and functional relationships for the potential groupings are not yet clear (Würsig and Clark, 1993; see Edds-Walton 1997 for review). In general, mysticete vocalizations are significantly lower in frequency than those of odontocetes (Table 1). Most mysticete signals are characterized as low frequency moans (0.4-40 seconds, fundamental frequency <<200 Hz); simple calls (impulsive, narrow band, peak frequency <1 kHz); complex calls (broadband pulsatile AM or FM signals); and complex "songs" with seasonal variations in phrasing and spectra (Thompson *et al.* 1979; Watkins 1981; Edds 1982,1988; Payne *et al.* 1983; Watkins and Wartzok 1985; Silber 1986; Clark 1990; Dahlheim and Ljungblad 1990). Infrasonic signals, typically in the 10 to 16 Hz range, are well documented in at least two species, the blue whale, *B. musculus* (Cummings and Thompson 1971; Edds 1982) and the fin whale, *B. physalus* (Watkins 1981; Edds 1982, 1988; Watkins *et al.* 1987). Suggestions that these low frequency signals are used for long distance communication and for topological imaging are intriguing but have not been definitively demonstrated.

*Pinnipeds*

The majority of pinniped sounds are in the sonic range but their signal characteristics are extremely diverse (Table 1). Some species are nearly silent, others have broad ranges and repertoires, and the form and rate of production vary seasonally, by sex, and whether the animal is in water or air (Watkins and Wartzok 1985; Richardson *et al.*, 1995). Calls have been described as grunts, barks, rasps, rattles, growls, creaky doors, and warbles in addition to the more conventional whistles, clicks, and pulses (Beier and Wartzok 1979, Ralls *et al.* 1985, Watkins and Wartzok 1985; Miller and Job 1992). Although clicks are produced, there is no clear evidence for echolocation in pinnipeds (Renouf *et al.* 1980, Schusterman 1981, Wartzok *et al.* 1984).

Phocid calls are commonly between 100 Hz and 15 kHz, with peak spectra <5 kHz but can range as high as 40 kHz. Typical source levels in water are estimated to be near 130 dB re 1 μPa, but levels as high as 193 dB re 1 μPa have been reported (Richardson *et al.* 1995). Infrasonic to seismic level vibrations are produced by northern elephant seals, *Mirounga angustirostris*, while vocalizing in air (Shipley *et al.* 1992).

Otariid calls are similarly variable in type, but most are in the 1-4 kHz range. The majority of sounds that have been analyzed are associated with social behaviors. Barks in water have slightly higher peak spectra than in air, although both center near 1.5 kHz. In-air harmonics that may be important in communication range up to 6 kHz. Schusterman *et al.* (1972), in their investigation of female California sea lion, *Zalophus californianus*, signature calls, found important inter-individual variations in call structure and showed that the calls have fundamental range characteristics consistent with peak in-air hearing sensitivities.

Odobenid sounds are generally in the low sonic range (fundamentals near 500 Hz; peak <2 kHz), and are commonly described as bell-like although whistles are also reported (Schevill *et al.* 1966, Ray and Watkins 1975, Verboom and Kastelein 1995).

*Sirenians*

Manatee, *Trichechus spp.*, and dugong, *Dugong dugon*, underwater sounds have been described as squeals, whistles, chirps, barks, trills, squeaks, and frog-like calls (Sonoda and Takemura 1973; Richardson *et al.*, 1995, Anderson and Barclay 1995) (Table 1). West Indian manatee calls, *T. manatus,* typically range 0.6 to 5 kHz (Schevill and Watkins 1965). Calls of Amazonian manatees, *T. inunguis*, a smaller species than the Florida manatee, are slightly higher with peak spectra near 10 kHz, although distress calls have been reported to have harmonics up to 35 kHz (Bullock *et al.* 1980). *D. dugon* calls range from 0.5 to 18 kHz with peak spectra between 1 and 8 kHz (Nishiwaki and Marsh 1985, Anderson and Barclay 1995).

*Fissipeds*

Descriptions of otter sounds are similar to those for pinnipeds and for terrestrial carnivores (Table 1); *i.e.*, growls, whines, snarls, and chuckles (Kenyon 1981). Richardson *et al.* (1995) indicate that underwater sound production analyses are not available but that in-air calls are in the 3 to 5 kHz range and are relatively intense.

## *In Vivo* Marine Mammal Audiometry

As indicated in the introduction, hearing capacity is usually expressed as an audiogram, a plot of sensitivity (threshold level in dB SPL) vs. frequency , which is obtained by behavioral or electrophysiological measures of hearing. Mammals typically have a U-shaped hearing curve. Sensitivity decreases on either side of a relatively narrow band of frequencies at which hearing is significantly more acute. The decline in sensitivity is generally steepest above the best frequency. Behavioral and neurophysiological hearing curves are generally similar, although behavioral audiograms typically have lower thresholds for peak sensitivities (Dallos *et al.* 1978). Inter-individual and inter-trial differences in audiograms may be related to variety of sources, including ear health, anaesthesia, masking by other sounds, timing, anticipation by the subject, etc.

Hearing curves are available for approximately 12 species of marine mammals (Figure 3) and have the same basic U-shaped pattern as land mammal curves. Peak sensitivities are generally consistent with the vocalization data in those species for which both data sets are available (compare Table 1, Figure 3). Detailed reviews of data for specific marine mammals are available in Bullock and Gurevich (1979), McCormick *et al.* (1980), Popper (1980), Schusterman (1981), Watkins and Wartzok (1985), Fay (1988), Awbrey (1990), Au (1993), and Richardson *et al.* (1995). Data discussed here for cetaceans and sirenians are limited to underwater measures. Most pinnipeds are in effect "amphibious" hearers in that they operate and presumably use sound in both air and water; therefore data are included from both media where available. No published audiometric data are available for mysticetes, marine otters, or polar bears.

*Cetaceans*

Hearing Range

Electrophysiological and behavioral audiograms are available for seven odontocete species (Au 1993), most of which are Type II delphinids with peak sensitivity in the 40-80 kHz range(Figure 3a). Data, generally from one individual, are available also for beluga whales (*Delphinapterus leucas*), *I. geoffrensis*, and *P. phocoena*. There are no published audiograms for the largest physeterids and ziphiids. The available data indicate that odontocetes tend to have at least a 10 octave functional hearing range, compared with 8-9 octaves in the majority of mammals. Best sensitivities ranged from 12 kHz in *O. orca*, (Schevill and Watkins 1966, Hall and Johnson 1971) to over 100 kHz in *I. geoffrensis* and *P. phocoena* (Voronov and Stosman 1977, Supin and Popov 1990, Møhl and Andersen 1973).

Resolution

Until recently, most odontocete audiometric work was directed at understanding echolocation abilities rather than underwater hearing *per se*. Much of what is known about odontocete hearing is therefore related to ultrasonic abilities. Acuity measures commonly used in these studies include operational signal strength, angular resolution, and difference limens. The first two are self explanatory. Difference limens (DL) are a measure of frequency discrimination based on the ability to differentiate between two frequencies or whether a single frequency is modulated. Difference limens are usually reported simply in terms of Hz or as relative difference limens (rdl), which are calculated as a percent equal to 100 times the DL in Hz/frequency. Au (1990) found that echolocation performance in *Tursiops* was 6 to 8 dB lower than that expected from an ideal receiver. Target detection thresholds as small as 5 cm at 5 meters have been reported, implying an auditory angular resolution ability of as little as ~0.5° although most data suggest 1° to 4° for horizontal and vertical resolution is more common (Bullock and Gurevich 1979, Popper 1980, Au 1990). Minimal intensity discrimination in *Tursiops* (1 dB) is equal to human values; temporal discrimination (~8% of signal duration) is superior to human. Frequency discrimination in *Tursiops* varies from 0.28 to 1.4% rdl for frequencies between 1-140 kHz; best values are found between 5 and 60 kHz (Popper, 1980). These values are similar to those of microchiropteran bats and superior to the human average (Grinnell 1963; Long 1980; Pollack 1980; Popper 1980; Sales and Pye 1974; Simmons 1973; Watkins and Wartzok 1985). Frequency discrimination and angular resolution in *Phocoena* (0.1-0.2% rdl; 0.5-1o) are on average better than for *Tursiops* (Popper 1980).

An important aspect of any sensory system for survival is the ability to detect relevant signals amidst background noise. Critical bands and critical ratios are two measures of the ability to detect signals embedded in noise, or the ear's resistance to masking. In hearing studies, the term "masking" refers to the phenomenon in which one sound eliminates or degrades the perception of another (see Yost 1994 for a detailed discussion). To measure a critical band, a test signal, the target (usually a pure tone), and a competing signal, the masker, are presented simultaneously. Fletcher (1940) showed that as the bandwidth of the masker narrows, the target suddenly becomes easier to detect. The critical band (CB) is the bandwidth at that point expressed as a percent of the center frequency. If the ear's frequency resolution is relatively poor, there is a broad skirt of frequencies around the target tone that can mask it, and the CB is large. If the ear has relatively good frequency resolution, the CB is relatively narrow. Critical ratios (CR) are a comparison of the signal power required for target detection vs. noise power, and are simply calculated as the threshold level of the target in noise (in dB) minus the masker level (dB). Critical bands tend to be a constant function of the critical ratios throughout an animal's functional hearing range. Consequently, CR measures with white noise, which are easier to obtain than CB's, have been used to calculate masking bandwidths based on the assumption that the noise power integrated over the critical band equals the power of the target at its detection threshold, or,

$$CB(Hz) = 10^{(CR/10)} \tag{7}$$

(Fletcher 1940, Fay 1992). This implies the target strength is at least equal to that of the noise, however, there are exceptions. Although uncommon, *negative* CR's, meaning the signal is detected at levels below the noise; have been reported for human detection of speech signals and for some bats near their echolocation frequencies (Schuknecht 1993, Kössl and Vater 1995). Typical values for human CR's at speech frequencies are 10-18 dB. Critical bands are thought to depend on stiffness variations in the inner ear. In generalist ears, the critical bandwidths are relatively constant at ~0.25 to 0.35 octaves/mm of basilar membrane (Ketten 1984, 1992; West 1985, 1986; Allen and Neeley 1992). Although hearing ranges vary widely in terms of frequency, most mammals have a hearing range of 8-9 octaves, which is consistent with earlier findings that the number of critical bands was approximately equal to basilar membrane length in mm (Pickles 1982, Greenwood 1990).

Based on critical ratio and critical band data, odontocetes are better than most mammals at detecting signals in noise. Odontocetes have more critical bands and the critical ratios are generally smaller than in humans. Further, odontocete critical bandwidths can approach 0 and are not a constant factor of the ratio at different frequencies. *T. truncatus* has 40 critical bands, which vary from 10 times the critical ratio at 30 kHz to 8 times the critical ratio at 120 kHz (Johnson 1968, 1971; Moore and Au 1983; Watkins and Wartzok 1985; Thomas *et al.* 1988, 1990b). Critical ratios for *Tursiops* (20 to 40 dB) are, however, generally higher than in other odontocetes measured. The best critical ratios to date (8 to 40 dB) are for the false killer whale, *Pseudorca crassidens*, (Thomas *et al.* 1990b), which is also the species that has performed best in echolocation discrimination tasks (Nachtigall *et al.* 1996).

Localization

Sound localization is an important aspect of hearing in which the medium has a profound effect. In land mammals, two cues are important for localizing sound: differences in arrival time (interaural time) and in sound level (interaural intensity). Binaural hearing studies are relatively rare for marine mammals, but the consensus from research on both pinnipeds and odontocetes is that binaural cues are important for underwater localization (Dudok van Heel 1962, Gentry 1967, Renaud and Popper 1975, Moore *et al.* 1995); however, because of sound speed differences, small or absent pinna, and ear canal adaptations in marine mammals, localization mechanisms may be somewhat different from those of land mammals.

In mammals, the high frequency limit of functional hearing in each species is correlated with its interaural time distance (IATD - the distance sound travels from one ear to the other divided by the speed of sound; Heffner and Masterton 1990). The narrower the head, the smaller the IATD, the higher the frequency an animal must perceive with good sensitivity to detect arrival time via phase differences. For example, consider a pure tone (sine wave) arriving at the head. If the sound is directly in front of the head, the sound will arrive at the same time and with the same phase at each ear. As the animal's head turns away from the source, each ear receives a different phase, given that the inter-ear distance is different from an even multiple of the wavelength of the sound. IATD cues therefore involve comparing time of arrival vs. phase differences at different frequencies in each ear. Phase cues are useful primarily at frequencies below the functional limit; however, the higher the frequency an animal can hear, the more likely it is to have good sensitivity at the upper end of frequency range for phase cues.

Clearly, interaural time distances depend upon the sound conduction path in the animal and the media through which sound travels. For terrestrial species, the normal sound path is through air, around the head, pinna to pinna. The key entry point for localization cues is the external auditory meatus, and the IATD is therefore the intermeatal (IM) distance measured around the head divided by the speed of sound in air. In aquatic animals, sound can travel in a straight line, by tissue conduction, through the head given that tissue impedances are similar to the impedance of sea water. Experiments with delphinids suggest that intercochlear (IC) or inter-jaw distances are the most appropriate measure for calculating IATD values in odontocetes (Dudok van Heel 1962; Renaud and Popper 1975; Moore *et al.* 1995). The IC distances of dolphins are acoustically equivalent to a rat or bat IM distance in air because of the increased speed of sound in water. Supin and Popov (1993) proposed that marine mammals without pinnae were incapable of using IATD cues, given the small inter-receptor distances implied by the inner ear as the alternative underwater receptor site. Recently, however, Moore *et al.* (1995) demonstrated that *Tursiops* has an IATD on the order of 7 μsec, which is better than the average human value (10 μsec) and well below that of most land mammals tested. If IM distances are used for land mammals and otariids in air and IC distances are used for cetaceans and underwater phocid data, marine mammal and land mammal data for IATD vs. high frequency limits follow similar trends (Ketten, 1997).

Intensity differences can be detected monaurally or binaurally, but binaural cues are most important for localizing high frequencies. In land mammals, intensity discrimination thresholds (ITD) are independent of frequency, decrease with increasing sound levels, and are generally better in larger animals (Fay 1992; Heffner and Heffner 1992). Humans and macaques commonly detect intensity differences of 0.5 to 2 dB throughout their functional hearing range; gerbils and chinchillas, 2.5 to 8 dB. Behavioral and evoked potential data show intensity differences are detectable by odontocetes at levels equal to those of land mammals and that the detection thresholds, like those of land mammals, decline with increasing sound level. Binaural behavioral studies and evoked potential recordings for *Tursiops* indicate an approximate IDT limit of 1-2 dB (Bullock *et al.* 1968, Moore *et al.*, 1995). In *Phocoena*, IDTs range 0.5 to 3 dB (Popov *et al.*. 1986). Thresholds in *Inia* range 3-5 dB (Supin and Popov 1993), but, again, because of small sample size and methodological differences, it is unclear whether these numbers represent true species differences. Fay (1992) points out that the IDT data for land mammals do not fit Weber's Law, which would predict a flat curve for IDT; *i.e.*, intensity discrimination in dB should be nearly constant. The fact that marine mammals differ in the same direction is intriguing. This could be a simple reflection of a common ancestral ear, but if the implication is that marine hearing organs evolved, re-evolved, or retained an ability to detect absolute rather than proportional differences, this suggests that there is substantial adaptive advantage for detecting subtle motion related differences or multiple sound sources at different locations.

Evoked Potentials

In the last decade, auditory evoked potential (AEP) or brainstem response (ABR) procedures have been established for odontocetes (Popov and Supin 1990a, Dolphin 1995). These techniques are highly suitable for studies with marine mammals for the same reasons they are widely used for measuring hearing in infants or debilitated humans, namely, they are rapid, minimally invasive, and require no training or active response by the subject. An acoustic stimulus is presented by ear or jaw phones and the evoked neural responses are recorded from surface electrodes or mini-electrodes inserted under the skin. The signals recorded reflect synchronous discharges of large populations of auditory neurons. ABR's consist of a series of 5 to 7 peaks or waves that occur within the first 10 ms following presentation of click or brief tone burst stimuli. Most mammals have similar ABR patterns, but there are clear species-specific differences in both latencies and amplitudes of each wave (Jewett 1970, Dallos *et al.* 1978, Achor and Starr 1980, Dolan *et al.* 1985, Shaw 1990). The delay and pattern of the waves are related to the source of the response. For example, wave I in most mammals is thought to derive from synchronous discharges of the auditory nerve; wave II from the auditory nerve or cochlear nucleus. ABRs from dolphins show clear species dependence. Typical ABRs from *Phocoena* and *Tursiops* have three positive peaks with increasing amplitudes, but those in *Phocoena* have longer latencies (Bullock *et al.* 1968, Ridgway *et al.* 1981, Bibikov 1992).

Recent work using continuous amplitude modulated stimuli (AMS) at low frequencies in *Tursiops* and *Pseudorca* suggest odontocetes can extract envelope features at higher modulation frequencies than other mammals (Kuwada *et al.* 1986, Dolphin and Mountain 1992, Dolphin 1995). Supin and Popov (1993) also showed that envelope following responses (EFR) are better measures of low frequency auditory activity than ABR. The anatomical correlates of EFRs have not been identified, but the data suggest auditory central nervous system adaptations in dolphins may include regions specialized for low as well as high frequencies.

*Pinnipeds*

Pinnipeds are particularly interesting because they are faced with two acoustic environments. Different ways for sensory information to be received and processed are required for equivalent air and water hearing in their amphibious lifestyle. One possibility is that pinnipeds have dual systems, operating independently for aquatic vs. air-borne stimuli. If this is the case, hearing might be expected to be equally acute but possibly have different frequency ranges related to behaviors in each medium; *e.g.*, feeding in water vs. the location of a pup on land. An alternative to the neffin-like dual but equal hearing is that pinnipeds are adapted primarily for one environment and have a "compromised" facility in the other. Renouf (1992) argued that there is an "*a priori* justification for expecting otariids and phocids" to operate with different sensory emphases given that phocids are more wholly aquatic. This question cannot be definitively resolved until more pinniped species have been tested. As with cetaceans, present data are limited to a few individuals from mostly smaller species. However, the most recent data suggest there are significant differences among pinnipeds in both their primary frequency adaptations and in their adaptations to air vs. water to warrant more wide-spread species research.

In-Water Hearing

Underwater behavioral audiograms for phocids are somewhat atypical in that the low frequency tail is relatively flat compared to other mammalian hearing curves (compare Figures, 2, Figure 3a, and Figure 3b; see also Fay 1988 or Yost 1994). In the phocids tested (harbor seal, *Phoca vitulina*; harp seal, *P. groenlandica*; ringed seal, *P. hispida*; monk seal, *Monachus schauinslandi*), peak sensitivities ranged between 10 and 30 kHz, with a functional high frequency limit of ~60 kHz, except for the monk seal which had a high frequency limit of 30 kHz (Schusterman 1981, Fay 1988, Thomas *et al.* 1990a). Low frequency functional limits are not yet well established for phocids, and it is likely that some of the apparent flatness will disappear as more animals are tested below 1 kHz. However, the fact that all phocid plots have remarkably little decrease in overall sensitivity below peak frequency is notable. Currently available data from an on-going study comparing *P. vitulina* and *M. angustirostris* hearing suggest that the elephant seal has significantly better underwater low frequency hearing thresholds than other pinnipeds tested to date (Kastak and Schusterman 1995, 1996).

In-Air Hearing

In-air audiograms for phocids have more conventional shapes with peak sensitivities at slightly lower frequencies (3-10 kHz) (Fay 1988; Kastak and Schusterman 1995, 1996). In-air evoked potential data on these species are consistent with behavioral results (Bullock *et al.* 1971; Dallos *et al.* 1978). In-air and underwater audiograms cannot be compared directly; however, when the data are converted to intensity measures, the thresholds for air-borne sounds are poorer, on average (Richardson *et al.* 1995), implying that phocids are primarily adapted for underwater hearing.

Resolution

Underwater audiograms and aerial audiograms are available for two species of otariids. Underwater hearing curves for California sea lions and northern fur seals, *Callorhinus ursinus*, have standard mammalian shapes. Functional underwater high frequency hearing limits for both species are between 35-40 kHz with peak sensitivities from 15-30 kHz (Fay 1988; Richardson *et al.* 1995). As with phocids, otariid peak sensitivities in air are shifted to lower frequencies ( <10 kHz; functional limit near 25 kHz), but there is relatively little difference in the overall in-air vs. underwater audiogram shape compared with phocids. The fact that the otariid aerial and underwater audiograms are relatively similar suggests that otariids may have developed parallel, equipotent hearing strategies for air and water or even, in the case of *Zalophus*, have "opted" evolutionarily for a slight edge in air.

Localization

In frequency discrimination and localization tasks, pinnipeds perform less well than odontocetes. Angular resolution ranges from 1.5° to 9°, with most animals performing in the 4° to 6° range (Møhl 1964, Bullock *et al.* 1971, Moore and Au 1975). There is wide individual variability and no consistent trend for aerial vs aquatic stimuli. Minimal intensity discrimination (3 dB) by *Zalophus* is poorer than that of dolphins or humans (Moore and Schusterman 1976); typical frequency discrimination limens for several phocids and the sea lion (1-2% rdl) (Møhl 1967, Schusterman and Moore 1978a, 1978b; Schusterman 1981) are similar to some of the bottlenosed dolphin data but are on average significantly larger (less sensitive) than those for harbor porpoise.

Critical ratio data are available for only three pinnipeds (Richardson *et al.* 1995). In the northern fur seal, underwater critical ratios measured over a fairly narrow range (2-30 kHz) were on a par with those of most odontocetes at those frequencies (18-35 dB). Critical ratios for one harbor seal in air and in water were generally similar but also had anomalously higher values for some data points. Data reported for the ringed seal were consistently 10 dB or more greater than those of the other two species; *i.e.*, significantly poorer than those of *Callorhinus* , *P. vitulina*, or most odontocetes. Turnbull and Terhune (1993) concluded that equivalent performances in air and water can be explained by having an external reception system (ear canal and middle ear) in which both signal and noise levels produce parallel impedance shifts. However, this implies an identical filter response in air and water, which means either identical processing or parallel but equally efficient paths in the two domains. That is, the ear canal and middle ear transfer functions remain constant regardless of the medium. Given the usual assumptions about the mechanisms underlying critical ratios, however, the results could also be attributed to a common inner ear response in both media.

Like odontocetes, pinnipeds in water have small acoustic inter-ear distances. It is not known whether they have specialized mechanisms for maintaining the external canal as the sound reception point underwater or if tissue conduction is used. Møhl and Ronald (1975), using cochlear microphonics, determined that in-air reception in the harp seal is via the external canal, but they also found that underwater the most sensitive region was located below the meatus in a region paralleling the canal. Pinnae allow monaural cues to be used; therefore, eared species may use two different strategies for localizing in air and in water.

*Sirenians*

Very little audiometric data are available for sirenians, the other obligate aquatic group. Published data for the West Indian manatee consist of one evoked potential study and preliminary reports from on-going work on manatee behavioral audiogram (Patton and Gerstein 1992; Gerstein *et al.* 1993; Gerstein 1994). Several evoked potential studies of *T. inunguis* have been published (Bullock *et al.* 1980, Klishin *et al.* 1990, Popov and Supin, 1990a) but no behavioral data. No audiometric data are available for dugongs.

Current behavioral data for *T. manatus* indicate a hearing range of approximately 0.1 to 40 kHz with best sensitivities near 16 kHz. Functional hearing limits within this range are not yet established. This octave distribution (7-8 octaves) is narrower than that of bottlenosed dolphins (10.5 octaves: 0.15 to 160 kHz; Au 1993) and phocid seals (8-9 octaves: 0.08-40 kHz; Kastak and Schusterman 1995, 1996) that have been tested over a wide range of frequencies. Best thresholds for manatees (50-55 dB re 1 μPa) are similar to in-water thresholds for several pinnipeds (45-55 dB re 1 μPa) but are significantly higher than those for odontocetes tested in similar conditions (30-40 dB re 1 μPa). An interesting feature of the manatee audiogram is that it is remarkably flat; *i.e.*, there is less than a 15 dB overall difference in thresholds between 5-20 kHz. In terms of level and shape, the *T. manatus* audiogram therefore more closely resembles the "essentially flat" audiograms of phocids noted by Richardson *et al.* (1995) than it does the sharply tuned curve typical of odontocetes. Bullock *et al.* (1982), using evoked potential techniques to measure *T. manatus* hearing, found a maximal upper frequency limit (35 kHz) that is similar to the behavioral results but a markedly different peak sensitivity (1.5 kHz). They also reported a sharp decline in response levels above 8 kHz.

Popov and Supin (1990a) found peak responses in evoked potential studies of *T. inunguis* between 5 and 10 kHz with thresholds of 60-90 dB re 1 μPa. Klishin *et al.* (1990) reported best sensitivities to underwater stimuli in *T. inunguis* to be between 7 and 12 kHz, based on auditory brainstem responses from awake animals.

*Fissipeds*

No conventional audiometric data are available for sea otters, *Enhydra lutris*. Behavioral measures of hearing in air for two North American river otters, *Lutra canadensis* (Gunn 1988) indicate a functional hearing range in air of approximately 0.45 to 35 kHz with peak sensitivity at 16 kHz, which is consistent with Spector's more general description of their hearing (1956).

## Mammalian Hearing Mechanisms: Functional Modeling

Hearing capacities are the output of the integrated components of the whole ear. All mammalian ears, including those of marine mammals, have three basic divisions: 1) an outer ear, 2) an air-filled middle ear with bony levers and membranes, and 3) a fluid-filled inner ear with mechanical resonators and sensory cells. The outer ear acts as a sound collector. The middle ear transforms acoustic components into mechanical ones detectable by the inner ear. The inner ear acts as a band-pass filter and mechano-chemical transducer of sound into neural impulses.

*Outer and Middle Ears*

The outer ear is subdivided conventionally into a pinna or ear flap that assists in localization, a funnel-shaped concha, and the ear canal or auditory tube. The size and shape of each component in each species is extraordinarily diverse, which makes any generalized statement about the function of the outer ear debatable. In most mammals, the pinnal flaps are distinct flanges that may be mobile. These flanges act as sound diffractors that aid in localization, primarily by acting as a funnel that selectively admits sounds along the pinnal axis (Heffner and Heffner 1992).

The middle ear is commonly described as an impedance-matching device or transformer that counteracts the ~36 dB loss from the impedance differences between air and the fluid-filled inner ear, an auditory hangover of vertebrate movement from water onto land. This gain is achieved by the mechanical advantages provided by the difference in the area of the middle ear membranes (large tympanic vs. small oval window) and by the lever ratio of the bony chain of middle ear ossicles which creates a pressure gain and a reduction in particle velocity at the inner ear.

Improving the efficiency of power transfer to the inner ear may not, however, be the only function for the middle ear. Recent studies on land mammals have led to a competing (but not mutually exclusive) theory called the peripheral filter-isopower function, in which the middle ear has a "tuning" role (see Zwislocki 1981, Rosowski 1994, Yost 1994 for comprehensive discussions). The middle ear is an air-filled cavity with significant differences among species in volume, stiffness (K), and mass (M). Each species has a characteristic middle ear resonance based on the combined chain of impedances, which, in turn, depends upon the mechanical properties of its middle ear components. For any animal, the sum of impedances is lowest; *i. e.*, middle ear admittance is greatest and energy transmission most efficient, at the middle ear's resonant frequency (f). As expected, this frequency also tends to be at or near the frequency with the lowest threshold (best sensitivity) for that species (Fay 1992).

Stiffness and mass have inverse effects on frequency in a resonant system:

$$f = (1/2\pi) \qquad (8)$$

Put another way, mass dominated systems have a lower resonant frequency than stiffness dominated systems. Increasing stiffness in any ear component (membranes, ossicles, cavity) improves the efficiency of transmission of high frequencies. Adding mass to the system, *e.g.*, by increasing cavity volume or increasing ossicular chain mass, favors low frequencies. Consequently, in addition to impedance matching, middle ears may be evolutionarily tuned as evidenced by different combinations of mass or stiffening agents in each species. Ultrasonic species like microchiropteran bats and dolphins have ossicular chains stiffened with bony struts and fused articulations (Reysenbach de Haan 1956, Pye 1972, Sales and Pye 1974, Ketten and Wartzok 1990). Low frequency species, like heteromyid desert rodents, mole rats, elephants, and mysticetes, have large, middle ears with flaccid tympanic membranes (Webster 1962; Hinchcliffe and Pye 1969; Webster and Webster 1975; Fleischer 1978; Ketten 1992, 1994).

*Inner Ear*

Mammalian inner ears are precocial; *i.e.*, they are structurally mature and functional at birth and may be active *in utero*. Inner ears are similarly tuned in that inner ear stiffness and mass characteristics are major determinants of species-specific hearing ranges. The inner ear consists of the cochlea (primary hearing receptor) and the vestibular system (organs of orientation and balance) (Fig. 4).

The cochlea is a fluid-filled spiral with a resonator, the basilar membrane, and a neuroreceptor, the Organ of Corti (Figure 5). When the basilar membrane moves, cilia on the hair cells of the Organ of Corti are deflected eliciting chemical changes that release neurotransmitters. Afferent fibers of the auditory nerve synapsing on the hair cells carry acoustic details to the brain, including frequency, amplitude, and temporal patterning, based on the location, degree of deflection, and sequencing of hair cells that are excited by basilar membrane motion. Efferent fibers also synapse with the hair cells, but their function is not yet fully understood. As discussed in the final sections, damage the hair cells is the primary mechanism underlying most hearing loss.

A key component in the cochlear system is the basilar membrane. Differences in hearing ranges are dictated largely by differences in stiffness and mass of the basilar membrane that are the result of basilar membrane thickness and width variations along the cochlear spiral. From base (closest the oval and round windows) to apex (farthest from the middle ear), changes in the construction of the basilar membrane in each mammal mechanically tune the ear to a specific set of frequencies (Figure 4). Each membrane region has a particular resonance characteristic and consequently greater deflection than other regions of the membrane for some input frequency. For any input signal within the hearing range of the animal, the entire basilar membrane will respond to some degree. At any one moment, each region of the membrane will have a different amount of deflection and a different phase related to the input signal. Over time, changes in amplitude and phase at each point give the impression of a traveling response wave along the cochlea, but because the membrane segments that have resonance characteristics closest to frequencies in the signal have greater displacements than other segments of the membrane, a characteristic profile or envelope develops for the signal. Figure 4 shows the place-dependent differences in the displacement envelopes that would occur in a generic mammalian inner ear for three pure-tone inputs.

Basilar membrane dimensions vary inversely, and generally regularly, with cochlear dimensions. The highest frequency each animal hears is encoded at the base of the cochlear spiral (near the oval window), where the membrane is narrow, thick, and stiff. Moving towards the apex of the spiral, as the membrane becomes broader and more pliant, progressively lower frequencies are encoded. Therefore, mammalian basilar membranes are essentially tonotopically arranged resonator arrays, ranging high to low from base to apex, rather like a guitar with densely packed strings graded to cover multiple octaves.

Recall that, in general, small mammals have good high frequency hearing characteristics and large mammals have comparatively low hearing ranges. Early inner ear models were based on the assumption that all mammalian basilar membranes were constructed of similar components that had a constant gradient with length and that length scaled with animal size. On average, smaller animals were assumed to have shorter, narrower, stiffer membranes while larger animals had longer membranes in which the majority of membrane modules were broader and less stiff (von Békésy 1960; Greenwood 1961, 1990). Given that assumption, frequency distributions in the inner ear of any species could be derived by comparing one parameter, basilar membrane length, with an arbitrary standard, the average human membrane length. For many land mammals, this assumption is correct, but only because length is an indirect correlate of other key features for basilar membrane resonance. For these ears, now termed "generalists" (Fay 1992; Echteler *et al.* 1994), basilar membrane thickness and width covary regularly with length; therefore, length can proportionately represent stiffness.

Only recently has it become clear that some species, termed "specialists" (Echteler *et al.* 1994), do not have the same thickness-width-length relationship as generalist land mammals (Manley 1972, Ketten 1984, 1997; West 1986). Most specialist animals have retuned their inner ears to fit an atypical tuning for their body size by either increasing mass to improve low frequency sensitivity in small ears (as in mole rats) or adding stiffening components to increase resonant frequencies in larger inner ears (as in dolphins) (Hinchcliffe and Pye 1969; Sales and Pye 1974; Webster and Webster 1975; Ketten 1984). The most extreme case of specialization is to be found in some bats which have relatively constant basilar membrane dimensions for ~30% of the cochlea and thereby devote a disproportionate amount of the membrane to encoding a very narrow band frequencies related to a component of their echolocation signal (Bruns and Schmieszek 1980, Vater 1988a, Kössl and Vater 1995).

## Structure-function-habitat links

Marine mammal ears fall into both categories and some species have a mix of generalist and specialist traits. Like land mammals, pinnipeds and cetaceans have basilar membranes that scale with animal size. Consequently, because marine mammals are relatively large, most have basilar membranes longer than the human average. If marine mammal ears followed the generalist land mammal pattern, most would have relatively poor ultrasonic hearing. For example, standard land mammal length-derived hearing models (Greenwood 1961, 1990; Fay 1992) predict an upper limit of hearing of ~16 kHz for bottlenosed dolphins, *Tursiops truncatus*, which actually have a functional high frequency hearing limit of 160 kHz (Au 1993). Prior to the discovery of dolphin echolocation, it was assumed that these large animals had predominately low functional hearing ranges similar to cows. Hearing is not constrained to low frequencies in marine mammals because they have radically different inner ear thickness-width gradients than generalist land mammals. In odontocetes, very high ultrasonic hearing is related also to the presence of extensive stiffening additions to the inner ear. These features, discussed in detail later in the document, demonstrate the usefulness of comparative audiometric and anatomical studies for teasing apart hearing mechanisms. In fact, one important outgrowth of marine mammal hearing studies has been the development of multi-feature hearing models that are better predictors of hearing characteristics for all mammals than traditional, single-dimension models (Ketten, 1994, 1997).

## Marine Mammal Ears: Functional Anatomy

All marine mammals have special adaptations of the external (closure, wall thickening, wax plugs) and middle ear (thickened middle ear mucosa, broad Eustachian tubes) consistent with deep, rapid diving and long-term submersion, but they retain an air-filled middle ear and have the same basic inner ear configuration as terrestrial species. Each group has distinct adaptations that correlate with both their hearing capacities and with their relative level of adaptation to water.

### *Cetaceans*

#### Outer Ear

Pinnae are absent, although vestigial pinnal rings occur in some individuals. External auditory canals are present in Cetacea, but it is debatable whether they are functional. In odontocetes, the external canal is exceptionally narrow and plugged with cellular debris and dense, waxy cerumen. The canal has no observable attachment to the tympanic membrane or the middle ear. In mysticetes, the canal is narrow along most of its length, but the proximal end flares, cloaking the "glove finger", a complex, thickened membrane capped by a waxy mound in adults (Reysenbach de Haan, 1956).

Reysenbach de Haan (1956) and Dudok van Heel (1962) were among the first researchers to suggest soft tissue paths as an alternative to conventional external canal sound conduction in odontocetes. Reysenbach de Haan (1956) reasoned that since the transmission characteristics of blubber and sea water are similar, using a canal occluded with multiple substances would be less efficient than conduction through body fat, fluid, or bone. Dudok van Heel (1962) found the minimum audible angle in *Tursiops* was more consistent with an interbullar critical interaural distance than with intermeatal distances and concluded the canal was irrelevant. A passive resonator system involving the teeth of the lower jaw has been suggested for delphinids (Goodson and Klinowska 1990), but this cannot be considered a general explanation because it cannot account for echolocation by relatively toothless species; *e.g.* the Monodontidae (narwhals and belugas) and Ziphiidae (pelagic beaked whales). Currently, the lower jaw is considered the primary reception path for ultrasonic signals in odontocetes. Norris (1968, 1980) observed that the odontocete lower jaw has two exceptional properties: a fatty core and a thin, ovoid "pan bone" area in the posterior third of the mandible. Norris (1969) speculated this mandibular fat channel acts as a preferential low impedance path to the middle ear and the pan bone as an acoustic window to the middle ear region.

Several forms of data support this hypothesis. The fats in the mandible are wax esters with acoustic impedances close to sea water (Varanasi and Malins 1971). Evoked responses and cochlear potentials in *Stenella* and *Tursiops* were significantly greater for sound stimuli above 20 kHz from transducers placed on or near the mandible (Bullock *et al.* 1968, McCormick *et al.* 1970). Measurements with implanted hydrophones in severed *Tursiops* heads found best transmission characteristics for sources directed into the pan bone (Norris and Harvey 1974).

Brill *et al.* (1988) found that encasing the lower jaw in neoprene significantly impaired performance in echolocation tasks. Some results disagreed, notably those by Popov and Supin (1990b) and Bullock *et al.* (1968), who found best thresholds for low to sonic frequencies near the external meatus. However, recent computerized tomographic and magnetic resonance imaging of dolphins revealed a second channel of similar fats lateral to the pan bone (Ketten 1994), which may explain the discrepancy in the data since the lateral fatty lobes are near the meatus in delphinids. No discreet soft tissue channels to the ear have as yet been identified in mysticetes.

Ear placement

The inner ear is housed in a periotic bone fused at one or more points to the tympanic, or middle ear bone. This "tympano-periotic" bullar complex is located outside the skull, which increases the acoustic separation of the middle and inner ears, as discussed earlier in the section on localization and interaural distances.

Odontocete tympano-periotics are suspended in a spongy mucosa, the peribullar plexus, by five or more sets of ligaments. This mucosal cushion and the lack of bony connections to the skull isolate the ear from bony sound conduction and hold the tympanic loosely in line with the mandibular fatty channels and pan bone.

In mysticetes, extensive bony flanges wedge the periotic against the skull. The tight coupling of these flanges to the skull suggests both bony and soft tissue sound conduction to the ear occur in baleen whales.

Middle Ear

Ossicles of odontocetes and mysticetes are large and dense, but have wide species variations in size, stiffness, and shape (Reysenbach de Haan 1956, Belkovich and Solntseva 1970, Solntseva 1971, Fleischer 1978). In odontocetes, a bony ridge, the processus gracilis, fuses the malleus to the wall of the tympanic and the interossicular joints are stiffened with ligaments and a membranous sheath. Mysticete ossicles are equally massive but have none of the high frequency related specializations of odontocetes. The ossicles are not fused to the bulla and the stapes is fully mobile. The mysticete middle ear cavity is substantially larger than that of any odontocete. Thus, the mysticete middle ear consists of a large, open cavity with massive ossicles that are loosely joined; i. e., a characteristically low frequency ear.

The middle ear cavity in both odontocetes and mysticetes is lined with a thick, vascularized fibrous sheet, the corpus cavernosum. Computerized tomography (CT) and magnetic resonance imaging (MRI) data suggest the intratympanic space is air-filled *in vivo* (Ketten 1994). If so, a potential acoustic difficulty for a diving mammal is that changing middle ear volumes may alter the resonance characteristics of the middle ear, and, in turn alter hearing sensitivity. Studies are underway with free-swimming beluga whales (S. Ridgway, personal communication) to test whether hearing thresholds change with depth. In light of the extensive innervation of the middle ear corpus cavernosum by the trigeminal nerve, one novel task proposed for the trigeminal in cetaceans has been to regulate middle ear volume (Ketten, 1992), which could also explain exceptionally large trigeminal fiber numbers in both odontocetes and mysticetes (Jansen and Jansen 1969, Morgane and Jacobs 1972).

There is no clear consensus on how cetacean middle ears function. Both conventional ossicular motion and translational bone conduction have been proposed for cetaceans (Lipatov and Solntseva 1972; Fleischer 1978; McCormick *et al.* 1970, 1980). Based on experiments with anesthetized *T. truncatus* and a Pacific white-sided dolphin, *Lagenorhynchus obliquidens*, McCormick *et al.* (1970, 1980) concluded that sound entering from the mandible by bone conduction produces a "relative motion" between the stapes and the cochlear capsule. In their procedure, immobilizing the ossicular chain decreased cochlear potentials, but disrupting the external canal and tympanum had no effect. Fleischer (1978) suggested the procedure introduced an artificial conduction pathway. From anatomical studies, he concluded sound from any path is translated through tympanic vibration to the ossicles which conventionally pulse the oval window. McCormick's theory assumes fixed or fused tympano-periotic joints; Fleischer's requires a mobile stapes, distensible round window, and flexible tympano-periotic symphyses. Both conclusions may have been confounded by experimental constraints: McCormick *et al.* (1970) had to disrupt the middle ear cavity to expose the ossicles, while Fleischer's data were subject to post-mortem and preservation artifacts. In addition, neither theory is completely compatible with the wide structural variability of cetacean middle ears. The question of middle ear mechanisms in cetaceans therefore remains open.

### Inner Ear

The cetacean periotic houses the membranous labyrinth of the inner ear, which is further subdivided into auditory and vestibular components.

### Vestibular System

In all Cetacea, the vestibular system is substantially smaller in volume than the cochlea (Boenninghaus 1903, Gray 1951, Ketten 1992, Gao and Zhou 1995). Although size is not a criterion for vestibular function, cetaceans are unique in having semicircular canals that are significantly smaller than the cochlear canal (Gray 1951, Jansen and Jansen 1969). Innervation is proportionately reduced as well; *i.e.*, on average, less than 5% of the cetacean VIIIth nerve is devoted to vestibular fibers, as compared to approximately 40% in other mammals (Ketten, 1997). No equivalent reduction of the vestibular system is known in any land mammal. A possible explanation is that fusion of the cervical vertebrae in Cetacea resulted in limited head movements, which resulted in fewer inputs to the vestibular system that led to a reduction of related vestibular receptors. This does not mean that cetaceans do not receive acceleration and gravity cues but rather that the neural "budget" for these cues is less. In land mammals, similar vestibular reductions have been approximated only by experimentation, disease, congenital absence of canals, or, in some extreme cases, through surgery as a cure for vertigo (Graybiel, 1964).

### Cochlea

All cetacean cochleae have three scalae or chambers like other mammals: scala media (also called the cochlear duct), scala tympani, and scala vestibuli. The scalae are parallel fluid-filled tubes. Scala vestibuli ends at the oval window; scala tympani, at the round window; and scala media, which contains the Organ of Corti, is a blind pouch between them. Detailed descriptions of odontocete cochlear ducts are available in Wever *et al.* (1971a, b, c, 1972), Ketten (1984, 1992, 1997), Ketten and Wartzok (1990), and Solntseva (1971, 1990). This section briefly summarize the histological findings and discusses in detail only the cochlear features which influence hearing ranges and sensitivity.

Odontocete cochleae differ significantly from other mammalian cochleae by having hypertrophied cochlear duct structures, extremely dense ganglion cell distributions, and unique basilar membrane dimensions. Wever *et al.* (1971a, 1971b, 1971c; 1972) found all cellular elements of the Organ of Corti in *Tursiops* and *Lagenorhynchus* were larger and denser than in other mammals. More recent studies reported hypertrophy of the inner ear in phocoenids and monodontids as well (Ketten 1984, 1990; Solntseva 1990). Most of the hypercellularity is associated with the support cells of the basilar membrane and with the stria vascularis which plays a major role in cochlear metabolism. Mysticete ears are less well-endowed cellularly, but this may be a reflection of preservation artifacts that are more common in baleen specimens because of greater difficulties in their collection and generally longer post-mortem times before they are preserved.

The fiber and ganglion cell counts for the auditory nerve are exceptional in all cetaceans (Table 2). Auditory ganglion cell totals are more than double those of humans in all species, but, more important, the innervation densities (neurons/mm basilar membrane) are two- to three-fold greater than in other mammals. Comparisons of the ratios of auditory, vestibular, and optic nerve fibers in cetaceans vs. representative land mammals (Table 2) underscore the hypertrophy of the cetacean auditory nerve. The vestibular to auditory ratios are approximately 1/10 that of land mammals. Optic to auditory ratios in Type II odontocetes and mysticetes are approximately half those of most land mammals (noting an exception for the exceptionally high human optic value), while those of Type I riverine odontocetes are an order of magnitude less.

Auditory ganglion cell densities in Type I odontocetes are particularly notable, averaging over 3000 cells/mm. The data imply a ganglion to hair cell ratio of nearly 6:1 for Type I species. In humans, the ratio is 2.4:1; in cats, 3:1; and in bats, the average is 4:1 (Firbas 1972, Bruns and Schmieszek 1980, Vater 1988b). Wever *et al.* (1971c) speculated that additional innervation is required primarily in the basal region to relay greater detail about ultrasonic signals to the CNS in echolocation analyses. Electrophysiological results are consistent with this speculation. CNS recordings in both porpoises and bats imply increased ganglion cells correspond to multiple response sets that are parallel processed at the central level. Bullock *et al.* (1968) found three distinct categories of response units in the inferior colliculus of dolphin brains; *i.e.*, those that were signal duration specific, those that responded to changes in signal rise time, and those that were specialized to short latencies with no frequency specificity. This division of signal properties among populations of neurons is consistent with, although not identical to, observations in bats of multiple categories of facilitation and analysis neurons (Schnitzler 1983, Suga 1983). The odontocete inner ear neural distribution data imply that equally extensive analyses of signal characteristics are performed by odontocete auditory systems as well. However, while high afferent ratios in odontocetes could be related to the complexity of information extracted from echolocation signals, this theory does not explain similar densities in mysticetes. The similarity of odontocete and mysticete innervations suggests that mysticetes may have equally complex processing but possibly for infra- rather than ultrasonic tasks.

## Inner Ear Structure-Hearing Correlates

The cetacean basilar membrane is a highly differentiated structure with substantial variations in length, thickness, and width (Figure 6). Basilar membrane lengths in Cetacea, like those of terrestrial mammals, scale isomorphically with body size. In Cetacea, cochlear length is correlated strongly with animal size ($0.8 < r < 0.95$), but there is no significant correlation for length and frequency (Ketten, 1992). Thickness and width, however, are strongly correlated with hearing capacity (Ketten 1984, Ketten and Wartzok 1990). In most odontocetes, basilar membrane width is 30 μm at the base and increases to 300 - 500 μm apically. Basal widths of odontocetes are similar to those of bats and one third that of humans (Firbas, 1972, Schuknecht and Gulya 1986). Odontocetes thicknesses typically range from 25 μm at the base to 5 μm at the apex. Therefore, a typical cross-section of an odontocete basilar membrane is square and dense at the base becoming rectangular apically. Mysticete membranes are thin rectangles throughout, varying in thickness between 7 μm at the base to 2 μm at the apex. Width gradients in mysticetes can be as great as in odontocetes with membranes in some species ranging from 100 μm at the base (similar to the base in humans) to 1600 μm at the apex. The apical widths in mysticetes are 3X that of human, 3-5X those of most odontocetes, and 1.2X that of elephants, which are known to perceive infrasonics (Payne *et al.* 1986).

Comparing bat, odontocete, and mysticete basilar membrane thickness to width (T:W) ratios is a good exercise in structure-function relationships. T:W ratios are consistent with the maximal high and low frequencies each species hears and with differences in their peak spectra (Ketten and Wartzok, 1990; Ketten, 1992; Ketten, 1997). Echolocators have significantly higher basal ratios than mysticetes, and odontocete ratios are higher than for bats in the basal regions where their ultrasonic echolocation signals are encoded. For example, *Phocoena*, a Type I odontocete, has a basal T:W ratio of 0.9 and a peak frequency of 130 kHz. *Tursiops*, a Type II odontocete, has a T:W ratio of 0.7 and a peak signal of 70 kHz, and *Rhinolophus*, a bat, a 0.3 T:W ratio and a 40 kHz echolocation signal. All three have terminal apical ratios near 0.01. Mysticete T:W ratios range from 0.1 at the base to ~0.001 at the apex; i. e., the mysticete basal ratios are equivalent to mid-apical ratios in the three echolocators and decrease steadily to a value one-tenth that of odontocetes at the apex. The exceptionally low apical ratio in Mysticeti is consistent with a broad, flaccid membrane that can encode infrasonics.

A striking feature of odontocete basilar membranes is their association with extensive outer bony laminae. In mammals, ossified outer spiral laminae are hallmarks of ultrasonic ears (Yamada 1953, Reysenbach de Haan 1956, Sales and Pye 1974, Ketten 1984). Thick outer bony laminae are present throughout the basal turn in all odontocetes, and the proportional extent of outer laminae is functionally correlated with odontocete ultrasonic frequency ranges (Ketten and Wartzok 1990). In the basal, high frequency region of the cochlea, odontocete basilar membranes resemble thick girders, stiffened by attachments at both margins to a rigid bony shelf. In Type I echolocators with peak frequencies above 100 kHz an outer lamina is present for 60% of the cochlear duct (Figure 6). Type II echolocators with lower peak frequencies have a bony anchor for ~30% of the duct. The Type I basilar membrane therefore is coupled tightly to a stiff ledge for twice as much of its length as a Type II membrane. If Type I and Type II membranes have similar thickness:width ratios, a Type I cochlea with longer outer laminae would have greater membrane stiffness and higher resonant frequencies than an equivalent position in a Type II membrane without bony support. Both membrane ratios and the extent or proportion of auxiliary bony membrane support are important mechanistic keys to how odontocetes achieve ultrasonic hearing despite ear size.

Both inner and outer laminae are present in mysticete cochleae but they are morphologically and functionally very different from those of odontocetes. Mysticete outer laminae are narrow spicules located on the outer edge of the spiral ligament. They do not attach to the basilar membrane. The broad, thin mysticete basilar membrane attaches only to a flexible spiral ligament. It is likely that the spike-like outer lamina in mysticetes is a remnant of an ancestral condition rather than a functional acoustic structure and that low basilar membrane ratios and large Organ of Corti mass are the principal structural determinants of mysticete hearing ranges. To date, few mysticete species have been analyzed for very low frequency sensitivity, but the inner and middle ear anatomy argues strongly that they are low to infrasonic specialists.

### *Pinnipeds*

#### Outer Ear

Pinniped ears are less derived than cetacean ears. The external pinnae are reduced or absent. Ear canal diameter and closure mechanisms vary widely in pinnipeds, and the exact role of the canal in submerged hearing has not clearly been determined. Otariids have essentially terrestrial, broad bore external canals with moderate to distinctive pinnae. Phocids, particularly *M. angustirostris*, spend more time in water than otariids and have only a vestigial cartilaginous meatal ring, no pinnae, and narrow ear canals (Ketten and Schusterman, unpublished). Although the phocids have no external pinna, it is not yet known which species normally have air-filled vs. partial to fully blocked external canals. No specialized soft tissue sound paths for underwater hearing been clearly demonstrated in seals.

An obvious amphibious adaptation in phocid ears is that the external canal is well-developed and has a ring of voluntary muscle that can close the meatus (Møhl 1967, Repenning 1972). It has been suggested that seal middle ears are capable of operating entirely liquid-filled (Repenning 1972) and that various soft tissue attachments to the ossicles are related to the operation of a liquid-filled middle ear or for enhancing high-frequency sensitivity in water (Ramprashad *et al.* 1972, Renouf 1992), but neither of these suggestions is consistent with the level of development of the external canal or the size and development of the Eustachian tube. Whether the external canal remains patent and air-filled, collapses, or becomes flooded during dives remains a heavily debated subject. The ear canal contains a corpus cavernosum (cavernous epithelium) analogous to that in the middle ear, which may close the canal and regulate air pressures during dives (Møhl 1968, Repenning 1972). There are strong theoretical arguments for each position. Flooding the canal would provide a low impedance channel to the tympanic membrane, but then directing sound input to only one window of the cochlea becomes a problem. If the middle ear is fluid-filled, the oval and round windows can receive simultaneous stimulation that would interfere with normal basilar membrane response. However, if the canal remains air-filled, it poses the problem of an impedance mismatch that could make the canal less efficient for sound conduction to the middle and inner ear than surrounding soft tissues when the animal is submerged. To date, there is no clear evidence for specialized soft tissues, like those found in odontocetes, and no direct measures of the shape of the ear canal when submerged.

The position and attachment to the skull of the tympanic and periotic bones in pinnipeds is not significantly different from that of land mammals. The middle ear space is encased in a tympanic bulla, a bulbous bony chamber with one soft-walled opening, the tympanic membrane. The tympanic bulla is fused to the periotic. Both have partially or fully ossified articulations with the skull. These connections are less rigid than those in some land mammals, but the ears are not as clearly detached (and acoustically isolated) as those of cetaceans.

### Middle Ear

Pinniped middle ears have a moderate layer of cavernous tissue, but it is less developed than that of cetaceans (Møhl 1968, Ramprashad *et al.* 1972, Repenning 1972, Fleischer 1978). Pinniped ossicular chains are diverse: those in otariids resemble terrestrial carnivores; ossicles of phocids are more massive but with large species variation in shape (Doran 1879, Fleischer 1978), which suggests a wider range of peak frequencies and more emphasis on lower frequency reception than in otariids. Although some authors indicate phocids have small eardrums (Repenning 1972) the size is not significantly different from that of equivalent mass land mammals. The oval and round window areas in terrestrial mammals are of approximately the same size. In pinnipeds, the oval window can be one-half to one-third the size of the round window. Eardrum to oval window ratios have been cited frequently as a factor in middle ear gain, but this association is still being debated (Rosowski, 1994), and depending upon the exact size distributions among these three membranes in each pinniped species, there could be wide differences in middle ear amplification among pinnipeds.

### Inner Ear

Relatively few pinniped inner ears have been investigated and published data that are available are largely descriptive (Ramprashad *et al.* 1972; Solntseva 1990). Most pinnipeds have inner ears that resemble terrestrial high frequency generalists; *i.e.*, multiple turn spirals with partial laminar support. Preliminary data on larger species suggest they may have some low frequency adaptations consistent with their size. There is no indication of extensive adaptation for either high ultrasonic or infrasonic hearing. Pinnipeds have one feature in common with cetaceans; *i.e.*, a large cochlear aqueduct. Møhl (1968) suggested that this would facilitate bone conduction, but the mechanism is not clear, nor is it consistent with equally large aqueducts in odontocetes.

## *Sirenians*

Anatomical studies of sirenian ears are largely descriptive (Robineau 1969, Fleischer 1978, Ketten *et al.* 1992). Like Cetacea, they have no pinnae. Also, the tympano-periotics are constructed of exceptionally dense bone, but like pinnipeds (and unlike odontocetes), manatee ear complexes are partly fused to the inner wall of the cranium. Neonate ears vary less than 20% in shape and size from adult specimens; consequently, the ear complex is disproportionately large in young manatees and can constitute 14% of skeletal weight (Domning and de Buffrénil 1991).

### Outer Ear

Exact sound reception paths are not known in manatees. The unusual anatomy of the zygomatic arch, combined with its relation to the squamosal and periotic have made it a frequent candidate for a sirenian analogue to the odontocete fat channels. The periotic is tied by a syndesmotic (mixed fibrous tissue and bone) joint to the squamosal which is fused to the zygomatic process which is, in turn, a highly convoluted, cartilaginous labyrinth filled with lipids. The zygomatic is, in effect, an inflated, oil-filled, bony sponge that has substantial mass but less stiffness than an equivalent process of compact bone (Domning and Hayek 1986, Ketten *et al.* 1992). In the Amazonian manatee, the best thresholds in evoked potential recordings were obtained from probes overlying this region (Bullock *et al.* 1980, Klishin *et al.* 1990), but no clear acoustic function has been demonstrated

### Middle Ear

The middle ear system of sirenians is large and mass dominated but the extreme density of the ossicles adds stiffness (Fleischer 1978, Ketten *et al.* 1992). The middle ear cavity, as in other marine mammals, is lined with a thick, vascularized fibrous sheet. The ossicles are loosely joined and the stapes is columnar, a shape that is common in reptiles but rare in mammals and possibly unique to manatees. The tympanic membrane is everted and supported by a distinctive keel on the malleus. Deeply bowed, everted tympanic membranes, epitomized by the fibrous "glove finger" in mysticetes, are common in marine mammals but are relatively rare in non-aquatic species. Like eardrum of cats, the manatee tympanic membrane has two distinct regions, implying membrane response patterns are frequency-dependent (Pickles 1982). The tympanic-oval window ratio is approximately 15:1 in *T. manatus* , which places it mid-way between that of humans and elephants (Ketten *et al.* 1992, Rosowski 1994). Chorda tympani, a branch of the facial nerve (cranial nerve VII) which traverses the middle ear cavity, is relatively large in manatees. It is crosses the middle ear but has no known auditory function. In humans, chorda tympani is ~10% of the facial nerve, conveys taste from the anterior two-thirds of the tongue, and carries parasympathetic pre-ganglionic fibers to the salivary glands. In *T. manatus*, chorda tympani forms 30% of the facial nerve bundle.

Inner Ear

The sirenian inner ear is a mixture of aquatic and land mammal features. Anatomically, *T. manatus* inner ears are relatively unspecialized. The cochlea has none of the obvious features related to ultra- or infra- sonic hearing found in cetacean ears. Basilar membrane structure and neural distributions are closer to those of pinnipeds or some land mammals than to those of cetaceans (Ketten *et al.* 1992). The outer osseous spiral lamina is small or absent and the basilar membrane has a small base to apex gradient. At the thickest basal point, the membrane is approximately 150 μm wide and 7 μm thick; apically it is 600 μm by 5 μm. The manatee therefore has a relatively small basilar membrane gradient compared to cetaceans, which is consistent with the audiometric profile and 7 octave hearing range recently reported for *T. manatus* (Gerstein *et al.* 1993). Spiral ganglion cell densities are low compared to odontocetes (500/mm), but auditory ganglion cell sizes (20 μm X 10 μm) are larger than those of many land mammals.

*Fissipeds*

Remarkably little is known about sea otter, *Enhydra lutris*, hearing even in comparison to the sirenians.

*E. lutris* has a well-defined external ear flap and a canal which is open at the surface. Kenyon (1981) indicated that the pinnal flange folds downward on dives, which suggests the canal is at least passively closed during dives, but there are no data on whether specialized valves are associated with the ear canal like those found in pinnipeds. Otter auditory bullae are attached to the skull and resemble those of pinnipeds. CT scans of *E. lutris* (Ketten, unpublished) show that their middle and inner ears are grossly configured like ears of similarly sized terrestrial carnivores, with the same orientation and 2.5 turn distribution. Spector (1956) and Gunn (1988) both indicated an upper frequency limit of 35 kHz for common river otters which have similar ear anatomy.

## Mechanisms of Acoustic Trauma

### Temporary and Permanent Threshold Shifts

Noise trauma is a well-investigated phenomenon for air-adapted ears (see Lehnhardt, 1986; Lipscomb, 1978; and Richardson, *et al.*, 1991 for reviews). For the sake of completeness in the following discussion, noise trauma has been divided into lethal and sublethal impacts. Lethal impacts are those that result in the immediate death or serious debilitation of the majority of animals in or near an intense source; i.e., profound injuries related to shock wave or blast effects which are not, technically, pure acoustic trauma. Lethal impacts are discussed briefly at the end of this section. Sublethal impacts are those in which a hearing loss is caused by exposures to sounds that exceed the ear's tolerance to some acoustic parameter; i.e., auditory damage occurs from metabolic exhaustion or over-extension of one or more inner ear components. Of course, sublethal impacts may ultimately be as devastating as lethal impacts, causing death indirectly through behavioural reactions, such as panic, as well as impaired foraging or predator detection, but the potential for this type of extended or delayed impact from any sound source is not well understood for any mammal.

To determine whether any one animal or species is subject to a sublethal noise impact from a particular sound requires understanding how its hearing abilities interact with that sound. Basically, any noise at some level has the ability to damage hearing by causing decreased sensitivity. The loss of sensitivity is called a threshold shift. Not all noises will produce equivalent damage at some constant exposure level. The extent and duration of a threshold shift depends upon the synergistic effect of several acoustic features, including how sensitive the subject is to the sound. Most recent research efforts have been directed at understanding the basics of how frequency, intensity, and duration of exposures interact to produce damage rather than interspecific differences: that is, what sounds, at what levels, for how long, or how often will commonly produce recoverable (TTS - Temporary Threshold Shift) vs permanently (PTS) hearing loss.

Three fundamental effects are known at this time:

1) the severity of the loss from any one signal may differ among species.
2) for pure tones, the loss centers around the incident frequency.
3) for all tones, at some balance of noise level and time, the loss is irreversible.

Hearing losses are recoverable (TTS - temporary threshold Shift) or permanent (PTS) primarily based on extent of *inner* ear damage the *received* sound causes (see Lipscomb 1978, Lehnhardt 1986, Richardson *et al.* 1991 for reviews). Temporary threshold shifts (TTS) will be broad or punctate, according to source characteristics. The majority of studies have been conducted with cats and rodents, using relatively long duration stimuli (> 1 hr.) and mid to low frequencies (1-4 kHz) (see Lehnhardt, 1986, for summary). Inner ear damage location and severity are correlated with the power spectrum of the signal in relation to the sensitivity of the animal. Virtually all studies show that losses are centered around the peak spectra of the source and are highly dependent upon the frequency sensitivity of the subject. For narrow band, high frequency signals, losses typically occur in or near the signal band, but intensity and duration can act synergistically to broaden the loss.

It has also been established that repeated exposures to TTS level stimuli without adequate recovery periods can induce permanent, acute threshold shifts. Liberman (1987) showed that losses were directly correlated with graded damage to the outer and inner hair cells, and that the majority of cells recover. With short duration, narrow band stimuli, recovery periods can vary from hours to days. In effect, the duration of a threshold shift, is correlated with both the length of time and the intensity of exposure. In general, if the duration to intense noise is short and the noise is narrow, the loss is limited and recoverable. Based on both the available experimental data and on human data from occupational hearing loss, moderate to protracted exposures to a signal intensity of 80 dB or more over the individual threshold at each frequency for land species is required for significant threshold shifts (see NIH./CDC, 1990; Yost, 1994 for overview). These findings led to the current allowable limit of 80-90 dB re 20 μPa for human workplace exposures for broad spectrum signals, as well as an allowance of the 3-5 dB increase in exposure as a trade-off for halving of exposure times (Lehnhardt, 1986). While the commonality of 80 dB suggests that TTS is a dynamic range dependent phenomenon which is probably related to fundamental mammalian inner ear mechanisms, this specific dB criterion for exposure limits cannot be supported nor refuted with current data for marine mammals, particularly since some marine species have inner ear adaptations that could alter these responses (see Marine Mammal Issues section).

Given the complex nature of the interaction of species-specific hearing parameters with each signal feature a simplistic rule for species dependent impacts based on any one acoustic feature or hearing characteristic is not possible, as is shown in a quick review of Table 3. Some broad trends do emerge, however, from inter-species comparisons of sources that induce TTS in air.

At the grossest level, TTS effects from approximately equivalent exposures appear to be inversely related to weight or mass; i.e., effects were less pronounced in humans than in cat or in chinchilla, but this may be a secondary effect of frequency sensitivities differing also with animal size. The majority of effects appear to be species independent, suggesting that basic cochlear mechanisms may be the dominating factor. Effects that were common to all species were the following:

1. Shifts were strongly dependent on interactions of timing, level, and frequency.
2. Cumulative or compound effects are common.
2. Asymptotic shifts appear to depend on similar metabolic and mechanical fatigue phenomena.
3. Hearing impaired individuals have approximately the same absolute exposure limit for TTS as unimpaired individuals, which is manifested in an apparently smaller exposure window prior to TTS.
4. Effects spread primarily upward in frequency, which is a reflection of the basilar membrane's tonotopic organization and the asymmetric distribution of the traveling wave envelope (Fig. 4).
5. Frequency discrimination is unaffected.
6. Temporal integration is reduced.

Effects that showed strong species dependence were:

1. Loss at a particular frequency are correlated with species sensitivity.
2. Losses at all frequencies are correlated with metabolic, hair cell, and neural differences throughout the cochlea.

The majority of PTS effects are minimally species dependent, but nevertheless equally complex. One important aspect of PTS is that signal rise-time and duration of peak pressure are significant factors. If the exposure is short, hearing is recoverable; if long, or has a sudden, intense onset and is broadband, hearing, particularly in the higher frequencies, can be permanently lost (PTS). Experimentally, PTS is induced with multi-hour exposures to narrow band noise. In humans, PTS results most often from protracted, repeat intense exposures (*e.g.*, occupational auditory hazards from background noise) or sudden onset of intense sounds (*e.g.*, rapid, repeat gun fire). Sharp rise-time signals have been shown also to produce broad spectrum PTS at lower intensities than slow onset signals both in air and in water (Lipscomb, 1978; Lehnhardt, 1986; Liberman, 1987). Hearing loss with aging (presbycusis) is the accumulation of PTS and TTS insults to the ear. Typically, high frequencies are lost first with the loss gradually spreading to lower frequencies over time.

In experiments, multi-hour exposures to narrow band noise are used to induce PTS. As noted above, most mammals with air-adapted ears incur losses when the signal is 80 dB over threshold. TTS has been produced in humans for frequencies between 0.7 and 5.6 kHz (our most sensitive range) from underwater sound sources when received levels were 150-180 dB re 1 μPa (Smith and Wojtowicz 1985, Smith *et al.* 1988). Taking into account differences in measurements of sound pressure in air vs. water (equations 4 and 5), these underwater levels are consistent with the 80-90 dB exposure levels that induce TTS in humans at similar frequencies in air. Sharp rise-time signals produce broad spectrum PTS at lower intensities than slow onset signals both in air and in water (Lipscomb 1978, Lehnhardt 1986).

### Blast Effects

Simple intensity related loss is not synonymous with blast injury. Acoustic trauma induced by sudden onset, loud noise ( a "blast" of sound) is not synonymous with blast trauma, nor are noise and blast effects of the same magnitude. Blast injuries generally result from a single exposure to an explosive shock wave which has a compressive phase with a few microseconds initial rise time to a massive pressure increase over ambient followed by a rarefactive wave in which pressure drops well below ambient.

Blast injuries may be reparable or permanent according to the severity of the exposure and are conventionally divided into three groups based on severity of symptoms, which parallel those of barotrauma:

| MILD - Recovery | MODERATE - Partial loss | SEVERE - Permanent loss - death |
|---|---|---|
| Pain | Otitis media | Ossicular Fracture/Dislocation |
| Vertigo | Tympanic membrane rupture | Round/Oval window rupture |
| Tinnitus | Tympanic membrane hematoma | CSF leakage into middle ear |
| Hearing Loss | Serum-blood in middle ear | Cochlear and saccular damage |
| Tympanic tear | Dissection of mucosa | |

Moderate to severe stages result most often from blasts, extreme intensity shifts, and trauma; i.e., explosions or blunt cranial impacts that cause sudden, massive systemic pressure increases and surges of circulatory or spinal fluid pressures (Schuknecht, 1993). Hearing loss in these cases results from an eruptive injury to the inner ear; i.e., with the rarefactive wave of a nearby explosion, cerebrospinal fluid pressures increase and the inner ear window membranes blow out due to pressure increases in the inner ear fluids. Inner ear damage frequently coincides with fractures to the bony capsule of the ear or middle ear bones and with rupture of the eardrum. Although technically a pressure induced injury, hearing loss and the accompanying gross structural damage to the ear from blasts are more appropriately thought of as the result of the inability of the ear to accommodate the sudden, extreme pressure differentials and over-pressures from the shock wave.

At increasing distance from the blast, the effects of the shock wave lessen and even though there is no overt tissue damage, mild damage with some permanent hearing loss occurs (Burdick, 1981, in Lehnhardt, 1986). This type of loss is generally called an asymptotic threshold shift (ATS) because, as was found with protracted exposures in TTS experiments, ATS derives from a saturation effect. Like TTS, the hair cells are damaged, but as in PTS, recovery is unlikely to take place. Because ATS depends upon complex interactions of rise time and wave form, not simply intensity at peak frequency, hearing losses are typically broader and more profound than simple PTS losses.

There is no well defined single criterion for sublethal ATS from blasts (Roberto, et al., 1989), but eardrum rupture, which is common to all stages of blast injury, has been moderately well investigated. Although rupture *per se* is not synonymous with permanent loss (eardrum ruptures have occurred at as little as 2.5 kPa overpressure and are strongly influenced by the health of the ear), the incidence of tympanic membrane rupture is strongly correlated with distance from the blast (Kerr, & Byrne, 1975). As frequency of rupture increases so does the incidence of permanent hearing loss. In zones where >50% tympanic membrane rupture occurred, 30% of the victims had long term or permanent loss.

Recent experimental work has shown that weighted sound exposure level is a more robust predictor of permanent loss than peak pressure (Patterson, 1991). Data with weighted levels are rare; overpressure data are more common and have been shown to be highly correlated with received levels (Roberto *et al., 1989*). In general, complex and fast-rise time sounds cause ruptures at lower overpressures than slow-rise time waveforms, and smaller mammals will be injured by lower pressures larger animals. Of the animals tested to date, sheep and pig have ears anatomically closest to those of whales and seals. The air-based data for pigs and sheep imply that overpressures <70 kPa are needed to induce 100% tympanic membrane rupture. However, cross-study/cross-species comparisons and extrapolations are risky because of radically different experimental conditions as well as differences in acoustic energy transmission in the air and water. The data available for submerged and aquatic animals imply that lower pressures in water than in air induce serious trauma (Myrick et al., 1989; see also summary in Richardson, *et al.* 1991). For submerged terrestrial mammals, lethal injuries have occurred at overpressures $\geq$55 kPa (Yelverton, 1973, in Myrick, et *al.*, 1989; Richmond, *et al.*, 1989). In a study of Hydromex blasts in Lake Erie the overpressure limit for 100% mortality for fish was 30 kPa (Chamberlain, 1976). The aquatic studies imply therefore that overpressures between 30 and 50 kPa are sufficient for a high incidence of severe blast injury. Minimal injury limits in both land and fish studies coincided with overpressures of 0.5 to 1 kPa.

## Marine Mammal Issues

Major impacts from noise can be divided into direct physiologic effects, such as permanent vs. temporary hearing loss, and those that are largely behavioral, such as masking, aversion, or attraction. Although there is no substantial research accomplished in any of these areas in marine mammals, behavioral effects have been at least preliminarily investigated through playback and audiometric experiments, while marine mammal susceptibility to physiologic hearing loss is virtually unexplored. Despite increasing concern over the effects on marine mammals of man-made sound in the oceans, we still have little direct information about what sound frequency-intensity combinations damage marine mammal ears, and at present there are insufficient data to accurately determine acoustic exposure guidelines for any marine mammal.

Is acoustic trauma even moderately debatable in marine mammals? Recalling the paradox mentioned earlier, there are a variety of reasons to hypothesize that marine mammals may have evolved useful adaptations related to noise trauma. Vocalizations levels in marine mammals are frequently cited as indicating high tolerance for intense sounds. Some whales and dolphins have been documented to produce sounds with source levels as high as 180 to 220 dB re 1 μPa (Richardson *et al.,* 1991; Au, 1993). Vocalizations are accepted indicators for perceptible frequencies because peak spectra of vocalizations are near best frequency of hearing in most species, but it is important to recall that the two are not normally precisely coincident.

It must be borne in mind also that animals, including humans, commonly produce sounds which would produce discomfort if they were received at the ear at levels equal to levels at the production site, and arguments that marine mammals, simply by nature of their size and tissue densities, can tolerate higher intensities are not persuasive. First, mammal ears are protected from self-generated sounds not only by intervening tissues (head shadow and impedance mismatches) but also by active mechanisms (eardrum and ossicular tensors). These mechanisms do not necessarily provide equal protection from externally generated sounds largely because the impact is not anticipated as it is in self-generated sounds. Our active mechanisms are initiated in coordination and in anticipation of our own sound production. Just as the level of a shout is not indicative of normal or tolerable human hearing thresholds, source level calculations for vocalizations recorded in the wild should not be viewed as reliable sensitivity measures. As was indicated earlier, while there is little question of anomalous dysfunction of the middle ear in pinnipeds, middle ear function continues to debated for cetaceans. However, it is very important to recall also that cetaceans do have very well developed middle ear anatomies, including stapedial ligaments (Ketten, 1984; 1992) which argues that they have the capability for middle ear attenuation responses. Further, the large head size of a whale is not acoustically exceptional when the differences in pressure and sound speed in water vs. air are taken into account. As noted earlier, ear separation in a bottle-nosed dolphin is acoustically equivalent to that of a rat when the distances are corrected for the speed of sound in water. Exactly how head size in water affects attenuation of incident sound at the inner ear has not been investigated and remains an important open question.

Data from several pilot studies may, however, provide some useful insights into both facets of the paradox. In one investigation (detailed below, Ketten et al, 1993; Lien et al. 1993), ears from humpbacks that died following underwater explosions had extensive mechanical trauma while animals that were several kilometers distant from the blasts and at the surface showed no significant behavioral effects. These findings indicate adaptations that prevent barotrauma do not provide special protection from severe auditory blast trauma, but it remains unclear whether lower intensity purely acoustic stimuli induce temporary and/or acute threshold shifts in marine mammals.

A second study compared inner ears from one long-term captive dolphin with a documented hearing loss with the ears of one juvenile and two young adult dolphins (Ketten et al., 1995). CT, MRI, and histologic studies of the oldest dolphin ears showed cell loss and laminar demineralization like that found in humans with presbycusis, the progressive sensorineural hearing loss that accompanies old age. The location and degree of neural degeneration in this animal implied a substantial, progressive, hearing loss beginning in the high frequency regions. This too is consistent with the pattern commonly observed in humans. Frequency-position estimates of the elder animal's hearing loss done blind; i.e., without prior knowledge of its audiogram, predicted a profound loss for all frequencies >58 kHz. A review of the animal's behavioral audiogram subsequently showed that over a 12 year period this dolphin's hearing curve shifted from normal threshold responses for all frequencies up to 165 kHz to no functional hearing over 60 kHz prior to his death at age 28. For this animal at least, the conclusion was that significant hearing loss had occurred attributable only to age-related changes in the ear. Similar significant differences in the hearing thresholds of two *Zalophus* have also been reported by Kastak and Schusterman (1995) that are consistent with age-related hearing differences between the animals but which are also consistent with protracted exposures to construction noise.

Micrographs from young adult dolphin ears show several important cochlear duct cellular adaptations that are markedly different from those of conventional land mammals and seals. Transmission electron micrographic studies revealed dolphins have active fibrocytes in the spiral ligament and four times as many cell layers in stria vascularis as any other mammal. The stria is considered to be the principal dictator of mammalian cochlear metabolism. If these results are confirmed in other dolphin ears, these structural differences could mean dolphins have faster hair cell recovery times than air adapted ears and may therefore be less subject to temporary threshold shifts than most land animals or pinnipeds.

Unfortunately, these data only beg the question. The problem of hearing loss has not been realistically considered prior to this point in any systematic way in any marine mammal. In fact, the most studied group, odontocetes, have generally been thought of as ideal underwater receivers. A captive animal's age or history is not normally considered in analyzing its auditory responses, and, in the absence of overt data (e.g., antibiotic therapy), we assume a test animal has a normal ear with representative responses for that species. It is not clear that this is both reasonable and realistic. Particularly when data are obtained from one animal, it is important to question whether that hearing curve is representative of the normal ear for that species. The pilot studies noted clearly suggest age and/or exposure to noise can significantly alter hearing in marine mammals. In fact, in some cases (compare the two curves shown in figure 3a for *Tursiops*), "individual differences" that are seen in "normal" audiograms for two animals from the same species may be the result of undetected hearing loss in on of the animals. The fact that some studies show losses in marine mammals consistent with age-related hearing changes and disease considerably complicates the diagnosis and assessment of hearing loss from anthropogenic sources based on small samplings of populations. Natural loss should be considered in any animal for which there is little or no history, therefore the finding of a single animal with some hearing decrement in the vicinity of a loud source cannot be taken as a clear indicator of a population level hazard from that source. On the other hand, because of the importance of hearing to these animals, it is also unlikely that a high incidence of loss will be normally found in any wild population, and a finding of substantial hearing loss from, for instance, a mass-stranding or fishery coincident with a long-term exposure to an intense source would be appropriate cause for significant concern.

Given the minimal state of marine mammal data, the only comprehensive database that can be brought to bear at this time for predicting physiologic impacts is from acoustic trauma studies of land mammals and fish.

Few reports exist that detail injuries in marine mammals from blast induced trauma. Bohne et al. (1985) reported on inner ear damage in Weddell seals that survived blasts, but they were unable to determine exposure levels or number of exposures for each animal. There are scattered reports of opportunistic examinations of animals exposed to large blasts, including one on otters with extensive trauma from nuclear explosions (Richardson *et al.*, 1991) that concluded that peak pressures of 100-300 psi were invariably lethal. Recently, several humpbacks exposed to TOVEX blasts were shown to have severe blast injuries (Ketten et al., 1993). TOVEX, like Hydromex, is a TNT clone explosive similar to HBX-1 with a detonation velocity of ~7500 m/sec (Ketten, 1994). Received levels in the humpbacks could not be calculated with confidence; however, the charge weights associated with the injuries ranged from 1700 to 5000 kg. The animals died within three days of the blásts, and the extent of the injuries found implied they were close to the blast site. Mechanical trauma in these ears included round window rupture, ossicular chain disruption, bloody effusion of the peribullar spaces, dissection of the middle ear mucosa with pooled sera, and bilateral periotic fractures. These observations are consistent with classic blast injuries reported in humans, particularly with victims near the source who had massive, precipitous increases in cerebrospinal fluid pressure and brain trauma. There was no evidence of ship collision or prior concussive injury in these humpbacks, and no similar abnormalities were found in ears from humpbacks not exposed to blasts. These findings imply that despite adaptations in whales and seals that minimize barotrauma, marine mammals are not immune to blast trauma. Given the similarities of seal and whale ears to land mammal ears, it is clear that explosions and the shock wave and intense transient sound field that result can produce both blast injury and acoustic trauma in marine animals. More important, even though the whale ear is ostensibly a fluid-to-fluid coupler, marine mammals, having retained an air-filled middle ear (Ketten, 1994), are subject to all ranges of compressive-rarefactive/blast injury.

The level of impact from blast will depend on both an animal's location and, at outer zones, on its sensitivity to the residual noise. Factors that are most important for trauma from explosive sources are the following:

1. Topography
2. Proximity of ear
3. Anatomy and health of ear
4. Charge weight and type
5. Rise time
6. Overpressure
7. Pressure and duration of positive pressure phase

Topographic effects for open ocean are minimal for most boat deployed sources. Surface reflections will have a significant effect on the blast and acoustic wave spread patterns at some depth that is largely dependent on detonation depth. This effect also complicates predictions of received levels for animals at surface or within the air-sea boundary layer.

The health of individual ears that may be impacted cannot be estimated in advance. It is reasonable to assume an average distribution. Many explosives (TNT clones and water-gel explosives;e.g., HBX, Tovex, etc.) currently in use have high detonation velocities and are therefore effectively an instantaneous onset, high peak pressure, broad spectrum blast. Consequently, effects of the acoustic signature and certainly of the blast wave from these charges are likely to be similar in all species in the target area; i.e., individual hearing ranges are largely irrelevant in assessing TTS/PTS and blast effects in the near field, except for those species that have no discrete air pockets.

Although multiple parameters are associated with both lethal and sublethal effects, virtually all studies agree fairly closely on baseline criteria for lethal or compulsory injury zones for fast-rise time, complex waveforms: ~ 30-50 kPa peak overpressure in water and > 180 dB re 20 μPa in air (~240 dB re 1 μPa in water), (Chamberlain, 1976; Yelverton and Richmond, 1981; Phillips *et al.*, 1989: Richmond, *et al.*,, 1989; Myrick, et *al.*,, 1989). If, for comparison, the lowest otter impact estimate were chosen (100 psi), the impact range is substantially greater. Depending upon this range of criteria, a lethal impact zone limit for a 1200 lb source could be placed at 40 m. (absolute minimum, land mammal) or 300 m (conservative estimate of 100 psi based on otter observations). For a 10,000 lb. charge, the equivalent min-max limits for a killing ground are 70 m to 800 m. If a conservative average overpressure of ~30 kPa is used as the criterion, the lethality limit for both large charges is approximately 100 m. in comparison to approximately 10 m. and 50 m. for the 9 and 50 lb. charges.

Criteria for differentiating PTS or ATS zones from TTS are less clear. For this discussion, peak pressures of ~150 psi, which are consistent with 50% incidence of eardrum rupture (30% hearing loss) in larger mammals were chosen to define PTS/ATS limits. For a 9 lb. charge, pressures that result in significant auditory damage can be expected along a long axis radius of nearly 50 m. from the source. For a 50 lb charge, the equivalent PTS/ATS radius is nearly 100 m. For the 1200 and 10,000 lb charges, the transitional lethal zones in which serious sublethal injury will predominate are estimated as 300 m and 750 m, respectively Beyond these zones, the relative incidence of PTS to TTS will largely depend on individual susceptibility. That is, the variables that will determine TTS vs PTS are highly dependent on both species-specific and individual ear factors.

There is consensus in the literature on the criteria for an outer limit for mild TTS zones. 5-15 psi is accepted as the frontier at which TTS and detectable injury become rare (Yelverton and Richmond, 1981; Smith et al., 1985, 1988; Myrick et al., 1989; Roberto et al, 1989). This is also the zone in which the greatest differences are found in effects among charge weights. For 9 lb. charges, moderate incidence of TTS may be expected up to 700 m from the epicenter; the 50 lb TTS zone could extend to 1600 m in contrast to a 5 and 10 km radius from the heavier charges before the acoustic impact could be expected to drop precipitously.

## Acoustic Devices, Fisheries, and Mitigation Measures

### Potential impacts

Although the remainder of this discussion is concerned with purely physiologic elements of the effects of sound, it is important first to note that acoustic trauma *per se* is only one side of a significant effect coin.

Acoustic trauma is a very real and appropriate physiologic concern. It is also one for which we can obtain a metric that will allow us to provide a usable limit. That is, given that we know sound level X induces TTS while Y induces PTS, for frequency Z in a specific species, we can apply these data to the estimated exposure curve for that species and determine its risk of hearing loss. As discussed earlier, this is the basic principle behind both the 80 dB/5 dB rule currently in use for workplace exposures. Because of the importance of hearing to marine mammals, understanding how man-made sources may impact that sense is an important and reasonable step towards minimizing adverse impacts from man-made sound sources in the oceans, but it is imperative that we employ a scientifically valid, marine specific meter-stick for underwater exposures.

Above all, it is equally important to consider that sub-trauma levels of sound can have profound effects on individual fitness that propogate to the population level. These effects can take the form of masking of important signals, including echolocation signals, intra-species communication, and predator-prey cues; of disrupting important behaviors through startle and repellence, or of acting as attractive nuisances, all of which may alter migration patterns or result in abandonment of important habitats. Unfortunately, these issues are beyond the scope of this document as well as the expertise of the author and therefore cannot be productively and responsibly discussed here. Nevertheless, it is important to at least note the concern, and above all to suggest that there is a substantial need for field monitoring of behaviors in wild populations in tandem with controlled studies directed at expanding our audiometric data and understanding of acoustic trauma mechanisms.

As indicated earlier, there are no discrete data at this time that provide a direct measure of acoustic impact from a calibrated, underwater sound source for any marine mammal. Preliminary data from work underway on captive cetaceans and pinnipeds (Ridgway, pers. comm.; Schusterman, pers. comm.) suggest that odontocetes may have asymptotic responses while pinnipeds are more similar to land mammals in their dynamic range for threshold shift effects. This response difference as well as the difference in hearing ranges - *if these data are shown to be robust* - suggest that pinnipeds are the more acoustically fragile group from most anthropogenic sound sources and that odontocetes are relatively immune or require substantially higher sound levels to incur TTS.

In terms of the specifics of tuna-marine mammal-echo-ranging device interactions, the principal acoustic concern is to determine a balance of frequencies vs. level vs. duty cycle that will effectively detect and census commercially viable schools at long ranges but will not repel the target species nor harm marine mammals within that sound field. To accomplish these goals it is necessary to determine and balance the following components:

1. What are the effective frequencies for longer range detection? Presumably this will require a moderately low frequency for maximizing distance of detection balanced against a need to detect relatively small targets.

2. What is the hearing curve of the target species for capture? This feature must be considered in order to avoid startle or repellent effects in the fish schools that are to be detected by the source.

3. What are the hearing curves for non-target species within the sound field? This has the same concern as the second component, with a different end objective; i.e., to avoid impact or harassment but is driven also by an additional desire to prevent long-term, multiple exposure effects that can compound the probability of hearing loss.

Put simply, the device must be able to detect fish without cueing them but at the same time avoid frequency-intensity-sensitivity combinations likely to impact non-targeted, acoustically fragile species. Detection devices proposed recently (see Nero, 1996; Rees, 1996; Denny et al. 1997) commonly employ frequencies in the low to mid-sonic ranges (50-5000 Hz) with a wide set of emission algorithms, including repeat pulsed signals, and, in at least one scenario, explosive/high intensity impulsive source. Source levels proposed vary widely but can range as high as 235 dB re 1 μPa at 1 m. These spectra are coincident with virtually all marine mammal hearing ranges, and ironically may be well perceived by at least some fish species. In fact, for clupeids, recent data show a coincident high frequency sensitivity that suggests convergence of predator and prey auditory systems at both mid-sonic (2-4 kHz) and ultrasonic (20-40 kHz) ranges (Popper, 1997). Rather than complicating the issue, this coincidence may prove beneficial by driving the frequency choice in the same direction; i.e., avoiding these frequencies may maximize the utility of the device for finding fish without disturbance of the school while minimizing the probability of its impact on marine mammals.

**Mitigation measures**

For all species, the first issue in the proposed devices is signal shape, or rise time and peak spectra. As discussed earlier, impulsive sound has substantial potential for inducing broad spectrum, compounded acoustic trauma; i.e., an impulsive source can produce greater threshold changes than a non-impulsive source with equivalent spectral characteristics. Consequently, impulse is a complicating feature that may exacerbate the impact. Conventional suggestions for minimizing such effects are to ramp the signal, narrow the spectra, lower the pressure, and/or alter the duty cycle to allow recovery and decrease impact. Once again, however, it must be recalled which, if any, of these measures is important to the marine mammal ear has not been determined.

Given that impulsive noise can be avoided, the question devolves largely to the coincidence of signal characteristics with species sensitivities. High intensity, ultrasonic devices of course have enormous potential for serious impact on virtually every odontocete and their deployment in pelagic fisheries raises the greatest concern after impulse or explosive sources. Such devices are relatively unlikely to be employed, however, because they are unsuitable for longer range detection. With high frequency sonic range devices, the possibility of profound impact from disruption or masking of odontocete communication signals must certainly be considered, as well as the possibility of coincident impacts to pinnipeds. Because the majority of devices proposed use frequencies below ultra or high sonic ranges, odontocetes may be the least likely to be impacted species. Most odontocetes have relatively sharp decreases in sensitivity below 2 kHz (see fig. 3). If frequencies below 2 kHz are employed with a non-impulsive wave-form, the potential for impacting odontocetes is likely to be drastically reduced, but it must also be borne in mind that it is non-zero. In every case, the difference between some to little or no significant physiologic impact will depend upon received levels at the individual ear. For the purposes of general discussion, a theoretical comparison is shown in Figure 7 for marine mammals audiograms compared with a human audiogram and with source levels of major anthropogenic underwater noise sources. Because mechanisms and onset levels of TTS and PTS are still unresolved for marine mammals, this curve is presented largely for the purposes of gross comparisons of spectra of different sources with animal hearing ranges and is not intended to suggest mitigation guidelines.

Mysticetes and the majority of pinnipeds have substantially greater potential than odontocetes for direct acoustic impact from low to mid-sonic range devices. However, depending upon the diving and foraging patterns of these animals in comparison to the sound field propagated to detect fish, the risks to mysticetes and the majority of pinnipeds may be substantially less than a simple sound analysis would imply. That is, given that substantial numbers of these marine mammal groups are either not present or are infrequently found in the areas of tuna fisheries, there is little probability of any one animal encountering a signal with an intensity and a period of time that will induce acoustic trauma, despite their better absolute sensitivity to the signal.

Mitigation, like estimation of impact, requires a case by case assessment. At this time we have insufficient data to accurately predetermine the underwater acoustic impact from any anthropogenic source. Consequently, it is not possible to definitively state what measures will ameliorate any one impact.

For the immediate future and in the absence of needed data, a best faith effort at mitigation must be founded on reasoned predictions from land mammal and the minimal marine mammal and fish data available. It is reasonable to expect, based on the similarities in ear architecture and in the shape of behavioral audiograms between marine and land mammals, that marine mammals will have similar threshold shift mechanisms and will sustain acute trauma through similar mechanical loads. Therefore, fast-rise impulse and explosive sources are likely to have greater or more profound impacts than narrow band, ramped sources. Similarly, we can expect that a signal that is shorter than the integration time constant of the odontocete, mysticete or pinniped ear or which has a long interpulse interval has less potential for impact than a protracted signal; however, simply pulsing the signal is not a sufficient strategy without considering adequate interpulse recovery time. Strategies, such as compression, that allow the signal to be near or below the noise floor are certainly worth exploring. Certainly, no single figure can be supplied for these values for all species. Because of the exceptional variety in marine mammals ears and the implications of this variety for diversity of hearing ranges, there is no single frequency or combination of pulse sequences that will prevent any impact. It is however, reasonable, because of species-specificities, to consider minimizing effects by avoiding overlap with the hearing characteristics of species that have the highest probability of encountering the signal for each device deployed.

**Research Needs**

To that end, substantially better audiometric data are required. This means more species must be tested, with an emphasis on obtaining audiograms on younger, clearly unimpaired animals and repeat measures from multiple animals. Too often our data base has be undermined by a single measure from an animal that may have some impairment. It is equally important to obtain some metric of the hearing impairments present in normal wild populations in order to avoid future over-estimates of impact from man-made sources. To obtain these data requires a three-pronged effort of behavioural audiograms, evoked potentials on live strandings, and post-mortem examination of ears to determination of the level of "natural" disease and to hone predictive models of hearing capacities. It should be noted also that equivalent auditory databases are lacking for most commercially important fish species. Again, all of the recommendations presented are applicable for the fish stocks of interest in this endeavor, and coordinated or tandem research on both the commercially targeted and protected species that may be impacted may be the most productive approach to the problem of determining an effective frequency range for a device that balances effectiveness in fish censusing against minimal impact.

The most pressing research need in terms of marine mammals is data from live animals on sound parameters that induce temporary threshold shift and aversive responses. Indirect benefits of behavioral experiments with live captive animals that address TTS will also test the hypotheses that cellular structure in the inner ear of odontocetes may be related to increased resistance to auditory trauma. Combined data from these two areas could assist in determining whether or to what extent back-projections from land mammal data are valid.

Biomedical techniques, such as ABR and functional MRI, offer considerable potential for rapidly obtaining mysticete and pinniped hearing curves. Evoked potential studies of stranded mysticetes are of considerable value but must also carry the caveat of determining how reliable is a result from a single animal that may be physiologically compromised. Post-mortem studies should be considered on any animal that is euthanized after an ABR with the goal of both providing data about the normality of the ear and supplying feedback to modeling studies of hearing ranges. Otoacoustic emission experiments are not considered to be a viable approach for cetaceans; they may provide basic hearing data in pinnipeds but are technically difficult.

Playback studies are a well-established technique but because of the uncertainties about individually received levels they may not considerably advance our knowledge of acoustic impact *per se* unless tied to dataloggers or very accurate assessments of the animal's sound field. Tagging and telemetry are valuable approaches particularly if linked to field or video documentation of behavior that is coordinated with recordings of incident sound levels at the animal. Telemetric measurement of physiological responses to sound; e.g., heart rate, may be valuable, but little is currently known of how to interpret the data in terms of long term impact.

Permanent threshold shift data may be obtainable by carefully designed experiments that expose post-mortem marine mammal specimens to either intense sound and explosive sources since these effects are largely detectable through physical changes in the inner ear. These studies would also substantially increase the species diversity of the available data base because most marine mammal species will not be testable with conventional live animal audiometric techniques. Lastly, because many impact models depend upon assumptions about received levels at the ear, these projections would clearly be enhanced by basic measures on specimens of the underwater acoustic transmission characteristics of marine mammal heads and ears.

## Summary

Marine mammals are acoustically diverse with wide variations not only in ear anatomy, but also in frequency range and amplitude sensitivity. In general their hearing is as acute as that of land mammals, and they have wider ranges. Although marine mammals exhibit habitat and size related hearing trends that parallel those of land mammals in that larger species tend to have lower frequency ranges than smaller species, the majority of species have some ultrasonic capability and there are multiple specialized, auditory adaptations in odontocetes that provide large species exceptional high frequency hearing capabilities. Both mysticetes and odontocetes appear to have soft tissue channels for sound conduction to the ear. Sirenians may have analogous adaptations. It remains unclear whether pinnipeds use soft tissue channels in addition to the air-filled external canal for sound reception. Comparisons of the hearing characteristics of otarids and phocids suggest that there are at least two types of pinniped ears, with phocids being better adapted for underwater hearing. Sea otter ears are the most similar to those of land mammals of all marine mammal ears that have been investigated, but they do have some aquatic-related features, and it is not known how well they hear underwater. No data are available on polar bear hearing.

All marine mammals have middle ears that are heavily modified structurally from those in terrestrial mammals in ways that reduce the probability of barotrauma. The end product is an acoustically sensitive ear that is simultaneously adapted to sustain moderately rapid and extreme pressure changes, and which appears capable of accommodating acoustic power relationships several magnitudes greater than in air. It is possible that these special adaptations may coincidentally provide acoustically protective mechanisms that lessen the risk of injury from high intensity noise, but no behavioral or psychometric studies are yet available that directly address this issue.

One irony of sensory system research is that the more tools we invent to explore animals and their senses the greater the hints we receive that our reach is still too short. How extensive is our research arm currently? We know marine mammals use frequencies we cannot hear but we can technologically detect and transduce their frequency range into something we can analyze. Tools that help us probe and visualize how marine mammal sounds are produced and processed, like fast biomedical imaging, are helpful but still comparatively limited. The anatomical sophistication and the extensive cortical space allotted to temporal divisions of the brain in virtually all cetaceans, including baleen whales, implies a more important role for auditory processing than we have previously expected. Our greatest short-coming is that we cannot yet measure or observe reliably and frequently in the truly relevant environment for marine mammals: at depth in a free-ranging animal but technology that will make these studies routine are rapidly becoming available - and ironically will certainly have to employ acoustics to obtain definitive answers.

## Literature Cited


Achor, J., and A. Starr. 1980. Auditory brainstem responses in the cat. II. Effects of lesions. Electroencephalography and Clinical Neurophysiology 48:174-190.

Akamatsu, T., Y. Hatakeyama, T. Kojima and H. Soeda. 1994. Echolocation rates of two harbor porpoises *Phocoena phocoena*. Marine Mammal Science 10:401411.

Allen, J.B., and S.T. Neely. 1992. Mircomechanical models of the cochlea. Physics Today 45(7):40-47.

Anderson, P.K., and R.M.K. Barclay. 1995. Acoustic signals of solitary dugongs: Physical characteristics and behavioral correlates. Journal of Mammalogy 76(4):1226-1237.

Anderson, S., and G. Pilleri. 1970. Audible sound production in captive *Platanista gangetica*. Investigations on Cetacea II:83-86.

Asselin, S., M.O. Hammill and C. Barrette. 1993. Underwater vocalizations of ice breeding grey seals. Canadian Journal of Zoology 71:2211-2219.

Au, W. W. L. 1990. Target detection in noise by echolocating dolphins. Pages 203-216 *in* J.A. Thomas and R.A. Kastelein, eds. Sensory abilities of cetaceans: Laboratory and field evidence. Plenum Press, New York.

Au, W. W. L. 1993. The Sonar of dolphins. Springer-Verlag, New York, N.Y.

Au W.W.L., D.A. Carder, R.H. Penner and B. Scronce. 1985. Demonstration of adaptation in Beluga whale echolocation signals. Journal of the Acoustical Society of America 772:726-730.

Au, W.W.L., R.W. Floyd, R.H. Penner, and A.E. Murchison. 1974. Measurement of echolocation signals of the Atlantic bottle-nosed dolphin, *Tursiops truncatus* Montagu, in open waters. Journal of the Acoustical Society of America 56:1280-1290.

Au, W.W.L., R.H. Penner and C.W. Turl. 1987. Propagation of beluga echolocation signals. Journal of the Acoustical Society of America 82:807-813.

Awbrey, F.T. 1990. Comparison of hearing abilities with characteristics of echolocation signals. Pages 427-433 *in* J.A. Thomas and R.A. Kastelein, eds. Sensory abilities of cetaceans: Laboratory and field evidence. Plenum Press, New York.

Awbrey, F.T., J.A. Thomas, W.E. Evans and S. Leatherwood. 1982. Ross Sea killer whale vocalizations: preliminary description and comparison with those of some Northern Hemisphere killer whales. Report of the International Whaling Commission 32:667-670.

Backus, R.H., and W.E. Schevill. 1966. *Physeter* clicks. Pages 510-527 *in* K. S. Norris, ed. Whales, dolphins and porpoises. University of California Press, Berkeley.

Barnes, L.G., D.P. Domning and C.E. Ray. 1985. Status of studies on fossil marine mammals. Marine Mammal Science 1:15-53.

Barnes, L.G., and E. Mitchell. 1978. Cetacea. Pages 582-602 *in* Evolution of African mammals. Edited by V.J. Maglio and H.B.S. Cooke. Harvard University Press, Cambridge, Mass.

Belkovich, V. M., and G.N. Solntseva, G.N. 1970. Anatomy and function of the ear in dolphins. U.S. Government Research Development Reports 70(11): 275-282 (read as English summary).

Bibikov, N.G. 1992. Auditory brainstem responses in the harbor porpoise *(Phocoena phocoena*). Pages 197-211 *in* J. Thomas, R. Kastelein and A.Y. Supin, eds. Marine mammal sensory systems. Plenum Press, New York.

Boenninghaus, G. 1903. Das Ohr des Zahnwales, zyugleich ein Beitrag zur Theorie der Schalleitung. Zoologische JahrbÅecher (abteilung fur anatomie und ontogenie der tiere) 17:189-360. (not read in original).

Bohne, B., J. Thomas, E. Yohe, and S. Stone. 1985 Examination of potential hearing damage in Weddell seals (*Leptonychotes weddelli*) in Mc Murdo Sound, Antarctica. Ant. J., 20: 174-176.

Breathnach, A. S. 1960. The cetacean central nervous system. Biological Review 35:187-230.

Brill, R L., M.L. Sevenich, T.J. Sullivan, J.D. Sustman and R.E. Witt. 1988. Behavioral evidence for hearing through the lower jaw by an echolocating dolphin, *Tursiops truncatus*. Marine Mammal Science 4:223-230.

Brownlee, S. 1983. Correlations between sounds and behavior in the Hawaiian spinner dolphin, *Stenella longirostris*, M.S. thesis, University of California, Santa Cruz.

Bruins, W. and R. Cawood, 1991 Blast injuries of the ear as a result of the Peterborough lorry explosion: 22 March 1989, J. Laryn. Otol., 105: 890-895.

Bruns, V., and E.T. Schmieszek. 1980. Cochlear innervation in the greater horseshoe bat: Demonstration of an acoustic fovea. Hearing Research 3:27-43.

Buerki, C.B., T.W. Cranford, K.M. Langan and K.L. Marten. 1989. Acoustic recordings from two stranded beaked whales in captivity. Page 10 *in* Abstracts of the 8th Biennial Conference on the Biology of Marine Mammals. Pacific Grove, CA, Dec. 1989.

Bullock, T. H., D.P. Domning and R.C. Best. 1980. Evoked brain potentials demonstrate hearing in a manatee (*Trichechus inunguis*). Journal of Mammalogy 61:130-133.

Bullock, T.H., A.D. Grinnell, E. Ikezono, K. Kameda, Y. Katsuki, M. Nomoto, O. Sato, N. Suga, and K. Yanagisawa. 1968. Electrophysiological studies of central auditory mechanisms in cetaceans. Zeitschrift für Vergleichende Physiologie 59: 117-156.

Bullock, T.H., and V.S. Gurevich. 1979. Soviet literature on the nervous system and psychobiology of cetaceans. International Review of Neurobiology 21:47-127.

Bullock, T.H., S. Ridgway and N. Suga. 1971 Acoustically evoked potentials in midbrain auditory structures in sea lions Pinnipedia. Zeitshchrift für Vergleichende Physiologie 74: 372-387.

Bullock, T.H., T.J. O'Shea, and M. C. McClune. 1982. Auditory evoked potentials in the West Indian manatee (Sirenia:*Trichechus manatus*) Journal of Comparative Physiology 148:547-554.

Busnel, R.-G., and A. Dziedzic. 1966a. Acoustic signals of the pilot whale *Globicephala melaena* and of the porpoises *Delphinus delphis* and *Phocoena phocoena*. Pages 607-646 *in* K.S. Norris, ed. Whales, dolphins and porpoises. University of California Press, Berkeley.

Busnel, R.-G., and A. Dziedzic. 1966b. Caractéristiques physiques de certains signaux acoustiques du Delphinid *Steno bredanensis*. Comptes Rendus Academie du Scientifique. Paris 262:143-146.

Busnel, R.-G., and A. Dziedzic. 1968. Caractéristiques physiques des signaux acoustiques de *Pseudorcacrassidens* Owen (Cetace Odontocete). Mammalia 32:I-5.

Busnel, R.-G., G. Pilleri and F.C. Fraser. 1968. Notes concernant le dauphin *Stenella styxx* Gray 1846. Extrait de Mammalia 32:192-203.

Busnel, R.-G., A. Dziedzic and G. Alcuri. 1974. Etudes préliminaires de signaux acoustiques du marsouin *Pontoporia blainvillei* Gervais et D'Orligny (Cetacea, Plantanistidae). Mammalia 38:449-459.

Caldwell, D.K., and M.C. Caldwell. 1970. Echolocation-type signals by two dolphins, genus Sotalia. Quarterly Journal of Florida Academy of Science 33:124-131.

Caldwell, D.K., and M.C. Caldwell. 1971a. Sounds produced by two rare cetaceans stranded in Florida. Cetology 4:1-6.

Caldwell, D.K., and M.C. Caldwell. 1971b. Underwater pulsed sounds produced by captive spotted dolphins, *Stenella plagiodon*. Cetology 1:1-7

Caldwell, D.K., and M.C. Caldwell. 1987. Underwater echolocaton-type clicks by captive stranded pygmy sperm whales, *Kogia breviceps*. Page 8 *in*: Abstracts of the 7th Biennial Conference on the Biology of Marine Mammals.

Caldwell, D.K., M.C. Caldwell and J.F. Miller. 1969. Three brief narrow-band sound emissions by a captive male Risso's dolphin, *Grampus griseus*. Los Angles County Museum of Natural History Foundation Technical Report 5. 6 Pages NTIS AD-693157.

Caldwell, M.C., and D.K. Caldwell. 1967. Intraspecific transfer of information via pulsed sound in captive odontocete cetaceans, *in* R-G. Busnel, ed. Animal Sonar Systems: Biology and bionics II. Laboratoire de Physiologie Acoustique, Jouy-en-Josas.

Caldwell, M.C., and D.K. Caldwell. 1968. Vocalization of naive captive dolphins in small groups. Science 159:1121-1123.

Caldwell, M.C., and D.K. Caldwell. 1969. Simultaneous but different narrowband sound emissions by a captive eastern Pacific pilot whale, *Globicephala scammoni*. Mammalia 33:505-508, 2 plates.

Caldwell, M.C., and D.K. Caldwell. 1971. Statistical evidence for individual signature whistles in Pacific whitesided dolphins, *Lagenorhynchus obliquidens*. Cetology, 3:1-9.

Caldwell, M.C., D.K. Caldwell and J.F. Miller. 1973. Statistical evidence for individual signature whistles in the spotted dolphin, *Stenella plagiodon*. Cetology 16:1-21.

Caldwell, M.C., D.K. Caldwell and P.L. Tyack. 1990. Review of the signature whistle hypothesis for the Atlantic bottlenose dolphin. Pages 199-234 *in* S. Leathewood and R.R. Reeves eds. The bottlenose dolphin. Academic Press, San Diego, CA.

Carder, D. and S. Ridgway. 1990 Auditory brainstem response in a neonatal sperm whale, 120th Meeting, Acoustical Society of America, J. Acous. Soc. Am., Vol. 88, Suppl. 1, p. s4.

Chamberlain, A.J., 1976 The Acute and Subacute Effects of Underwater Rock Blasting, Dredging, and Other Construction Activity on the Fishes of the Nanticoke Region of Long Point Bay, Lake Erie, Ontario Ministry of Natural Resources. pp 132-143

Chapman, H.C. 1875. Observations on the structure of the manatee. Academy of Natural Sciences, Philadelphia, Proceedings 1872:452-462.

Clark, C. W. 1990. Acoustic behavior of mysticete whales. Pages 571-584 *in* J.A. Thomas and R.A. Kastelein, eds. Sensory abilities of cetaceans: Laboratory and field evidence. Plenum Press, New York.

Cummings, W.C., and J.F. Fish. 1971. A synopsis of marine animal underwater sounds in eight geographic areas. U.S. Naval Undersea Research & Development Center 97 pages NTIS AD-AO68875.

Cummings, W.C., and P.O. Thompson. 1971. Underwater sounds from the blue whale, *Balaenoptera musculus*, Journal of the Acoustical Society of America 50:1193-1198.

Cummings, W.C., D.V. Holliday and B.J. Lee. 1984 [publ. 1986]. Potential impacts of man-made noise on ringed seals: Vocalizations and reactions. Outer Continental Shelf Environmental Assessment Program, Final Report Principal Investigator, NOAA, Anchorage, AK 37:95-230. 693 pages OCS Study MMS 86-0021; NTIS PB87-107546.

Cummings, W.C., D.V. Holliday., W.T. Ellison and B.J. Graham. 1983. Technical feasibility of passive acoustic location of bowhead whales in population studies off Point Barrow, Alaska. T-83-06-002. Report from Tracor Applied Science, San Diego, CA for North Slope Borough, Barrow, AK.

Czaban, Z.J., P. Atchison, and J. Costain. 1994 Report on the underwater noise generated by the CPF shock trial, NDF document, Ottawa, Ontario.

Dahlheim, M.E., and D.K. Ljungblad. 1990. Preliminary hearing study on gray whales *Eschrictius robustus* in the field. Pages 335-346 *in* J.A. Thomas and R.A. Kastelein, eds. Sensory abilities of cetaceans: Laboratory and field evidence. Plenum Press, New York.

Dallos, P., D. Harris, O. Ozdamar and A. Ryan. 1978. Behavioral, compound action potential, and single unit thresholds: Relationship in normal and abnormal ears, Journal of the Acoustocal Society of America 64:151-157.

Dawson, S.M. 1988. The high frequency sounds of free-ranging Hector's dolphins, *Cephalorhynchus hectori*. Reports of the International Whaling Commission (Special Issue 9):339-344.

Dawson, S.M., and C.W. Thorpe. 1990. A quantitative analysis of the sounds of Hector's dolphin. Ethology 86:131-145.

Denny, G.F., K.E. deVilleroy, and P.K. Simpson. 1997. Long-Range Tuna School Detection Sonar System Design Specification. NOAA technical report no. NA77FD0044.

Diercks, K.J. 1972. Biological sonar systems: A bionics survey, Applied Research Laboratories, ARL-TR-72-34, University of Texas.

Diercks, K.J., R.T. Trochta, R.L. Greenlaw and W.E. Evans. 1971. Recording and analysis of dolphin echolocation signals. Journal of the Acoustical Society of America, 49:1729-1732.

Dolan, T.G., J.H. Mills and R.A. Schmidt. 1985. A comparison of brainstem, whole nerve and single-fiber tuning curves in the gerbils: Normative data. Hearing Research 17:259-266.
Dolphin, W.F. 1995. Steady-state auditory-evoked potentials in three cetacean species elicited using amplitude-modulated stimuli. Pages 25-47 *in* R.A. Kastelein, J.A. Thomas and P.E. Nachtigall, eds. Sensory systems of aquatic mammals. DeSpil Publishers, Woerden, Netherlands.
Dolphin, W.F., and D.C. Mountain. 1992. The envelope following response: Scalp potential elicited in the Mongolian gerbil using SAM acoustic stimuli. Hearing Research 58:70-78.
Domning, D. P. 1977. An ecological model for late Tertiary sirenian evolution in the North Pacific Ocean. Systematic Zoology 25:352-362.
Domning, D. P. 1981. Sea cows and sea grasses. Paleobiology 7:417-420.
Domning, D. P., and L.C. Hayek. 1986. Interspecific and intraspecific morphological variation in manatees (Sirenia: *Trichechus*). Marine Mammal Science 2:87-144.
Domning, D. P., and V. de Buffrénil. 1991. Hydrostasis in the Sirenia: Quantitative data and functional interpretations. Marine Mammal Science 7:331-368.
Domning, D. P., G.S. Morgan and C.E. Ray. 1982. North American Eocene sea cows (Mammalia: Sirenia). Smithsonian Contributions to Paleobiology 52:1-69.
Doran, A.H.G. 1879. Morphology of the mammalian ossicula auditus. Transactions of the Linnaean Society 1:371-497.
Dudok van Heel, W.H. 1962. Sound and cetacea. Netherlands Journal of Sea Research 1:407-507.
Dykes, R. W. 1975. Afferent fibers from mystacial vibrissae of cats and seals. Journal of Neurophysiology 38:650-662.
Dziedzic, A., and V. De Buffrenil. 1989. Acoustic signals of the Commerson's dolphin, *Cephalorhynchus commersonii*, in the Kerguelen Islands. Journal of Mammalogy 70:449-452.
Dziedzic, Z.-A. 1978. Etude experimentale des émissions sonar de certain delphinides et notamment de *D. delphis* et *T. truncatus*. Thèse de Doctorat d'Etat Es-Sciences Appliquées, l'Université de Paris VII.
Echteler, S.W., R.R. Fay and A.N. Popper. 1994. Structure of the mammalian cochlea. Pages 134-171 *in* R.R. Fay and A.N. Popper, eds. Comparative hearing: mammals. Springer-Verlag, New York, N.Y.
Edds, P. L. 1982. Vocalizations of the blue whale, *Balaenoptera musculus*, in the St Lawrence River. Journal of Mammalogy 63:345-347.
Edds, P.L. 1988. Characteristics of finback *Balaenoptera physalus* vocalizations in the St. Lawrence Estuary. Bioacoustics 1:131-149.
Edds-Walton, P.L. 1997. Acoustic communication signals of mysticete whales. Bioacoustics 47-60.
Eva, A. N. 1980. Pre-Miocene seagrass communities in the Caribbean, Palaeontology 23:231-236.
Evans, W.E. 1967. Vocalizations among marine mammals Pages 159-186 *in* Tavolga, ed. Marine Bio-Acoustics. W.N. Pergamon, New York.
Evans, W.E. 1973. Echolocation by marine delphinids and one species of fresh water dolphin. Journal of the Acoustical Society of America 54:191-199.
Evans, W.E., and E.S. Herald. 1970. Underwater calls of a captive Amazon manatee, *Trichechus inuguis*. Journal of Mammology 51:820-823.
Evans, W.E., and F.T. Awbrey. 1984. High frequency pulses of Commerson's dolphin and Dall's porpoise American Zoologist 24:2A.
Evans, W.E., and J.H. Prescott. 1962. Observations of the sound production capabilities of the bottlenose porpoise: A study of whistles and clicks, Zoologica 47:121-128.
Evans, W.E., F.T. Awbrey and H. Hackbarth. 1988. High frequency pulses produced by free-ranging Commerson's dolphin *Cephalorhynchus commersonii* compared to those of phocoenids. Reports of the International Whaling Commission (Special Issue 9):173-181.

Fay, R.R. 1988. Hearing vertebrates: A psychophysics databook. Hill-Fay Associates Winnetka, IL.
Fay, R.R. 1992. Structure and function in sound discrimination among vertebrates. Pages 229-267 *in* D.B. Webster, R.R. Fay and A.N. Popper, eds. The evolutionary biology of hearing. Springer-Verlag, New York, N.Y.
Firbas, W. 1972. Über anatomische Anpassungen des Hörorgans an die Aufnahme hîher Frequenzen. Monatszeitschrift Ohrenheilkd Laryngo-Rhinologie, 106:105-156
Fish, J.F., and C.W. Turl. 1976. Acoustic source levels of four species of small whales. NUC TP 547. U.S. Naval Undersea Center, San Diego, CA. 14 p. NTIS AD-A037620.
Fleischer, G. 1978. Evolutionary principles of the mammalian middle ear. Advanced Anatomy, Embryology and Cell Biology 55:1-70.
Fletcher, H. 1940. Auditory patterns. Reviews of Modern Physics 12:47-65.
Ford, J.K.B., and H.D. Fisher. 1978. Underwater acoustic signals of the narwhal *Monodon monoceros*. Canadian Journal of Zoology 56:552-560.
Ford, J.K.B., and H.D. Fisher. 1983. Group-specific dialects of killer whales *Orcinus orca* in British Columbia. Pages 129-161 *in* R. Payne, ed. Communication and behavior of whales. AAAS Sel. Symposium 76. Westview Press, Boulder, CO.
Friedl, W. A., P. E. Nachtigall, P. W. B. Moore, N. K. W. Chun, J. E. Haun, R. W. Hall and J. L. Richards. 1990. Taste reception in the Pacific bottlenose dolphin (*Tursiops truncatus gilli*) and the California sea lion (*Zalophus californianus*). Pages 447-454 *in* J. A. Thomas and R. A. Kastelein, eds. Sensory abilities of cetaceans: Laboratory and field evidence. Plenum, New York.
Gacek, R.R., and G.L. Rasmussen. 1961 Fiber analysis of the statoacoustic nerve of guinea pig, cat, and monkey. Anatomical Record 139;455.
Gao, A., and K. Zhou. 1987. On the retinal ganglion cells of *Neophocaena* and *Lipotes*. Acta Zoologica Sinica 33:316-323.
Gao, G., and K. Zhou. 1991. The number of fibers and range of fiber diameters in the cochlear nerve of three odontocete species. Canadian Journal of Zoology 69:2360-2364.
Gao, G., and K. Zhou. 1992. . Fiber analysis of the optic and cochlear nerves of small cetaceans. Pages 39-52 *in* J.A. Thomas, R.. A. Kastelein, and A. Supin, eds. Marine Mammal Sensory Systems. Plenum Press, New York.
Gao, G., and K. Zhou. 1995. Fiber analysis of the vestibular nerve of small cetaceans. Pages 447- 453 *in* R.A. Kastelein, J.A. Thomas, and P.E. Nachtigall, eds. Sensory systems of aquatic mammals. DeSpil, Woerden, Netherlands.
Gaskin, D.E. 1976. The Evolution, Zoogeography, and Ecology of Cetacea. Oceanography and Marine Biology: Annual Review, 14:247-346.
Gentry, R.L. 1967. Underwater auditory localization in the California sea lion (*Zalophus californianus*). Journal of Auditory Research 7:187-193.
Gerstein, E. R. 1994. Hearing Abilities of the West Indian Manatee, *Trichechus manatus*. Technical Report no. 119, Florida Inland Navigation District. 46 pp.
Gerstein, E.R., L.A. Gerstein, S.E. Forsythe and J.E. Blue. 1993. Underwater audiogram of a West Indian manatee *Trichechus manatus*. Page 130 *in* Abstract of the 10th Biennial Conference on Marine Mammals, Galveston, TX, November 1993.
Goodson, A.D., and M. Klinowska. 1990. A proposed echolocation receptor for the bottlenose dolphin (*Tursiops truncatus)*: Modeling the received directivity from tooth and lower jaw geometry. Pages 255-269 *in* J.A. Thomas and R.A. Kastelein, eds. Sensory abilities of cetaceans: Laboratory and field evidence. Plenum Press, New York.
Gray, O. 1951. An introduction to the study of the comparative anatomy of the labyrinth. Journal of Laryngology and Otology 65:681-703.
Graybiel, A. 1964. Vestibular sickness and some of its implications for space flight. Pages *in* W.S. Fields and R.R. Alford, eds. Neurological aspects of auditory and vestibular disorders. Charles C. Thomas, Springfield.
Greenwood, D.G. 1961. Critical bandwidth and the frequency coordinates of the basilar membrane. Journal of the Acoustical Society of America 33:1344-1356.

Greenwood, D.G. 1962. Approximate calculation of the dimensions of traveling-wave envelopes in four species. Journal of the Acoustical Society of America 34:1364-1384.

Greenwood, D. G. 1990. A cochlear frequency-position function for several species - 29 years later. Journal of the Acoustical Society of America 87:2592-2605.

Grinnell, A.D. 1963. The neurophysiology of audition in bats: Intensity and frequency parameters. Journal of Physiology 167:38-66.

Gunn, L.M. 1988. A Behavioral audiogram of the north American river otter (*Lutra canadensis*). M.Sc. thesis. San Diego State University, San Diego, Calif., 40 pp.

Hall, J. and C.S. Johnson. 1971. Auditory thresholds of a killer whale, *Orcinus orca* Linnaeus. Journal of the Acoustical Society of America 51:515-517.

Hanggi, E.B., and R.J. Schusteman. 1992. Underwater acoustic displays by male harbor seals *Phoca vitulina*. Initial results. Pages 449-457 *in* J.A. Thomas, R.A. Kastelein and A.Ya. Supin, eds. Marine mammal sensory systems. Plenum, New York.

Hanggi, E.B., and R.J. Schusterman. 1994. Underwater acoustic displays and individual variation in male harbor seals, *Phoca vitulina*. Animal Behavior 48:1275-1283.

Harrison, R. J., and G. L. Kooyman. 1968. General physiology of the pinnipeds. Pages 212-296 *in* R. J. Harrison, R.C. Hubbard, R.S. Peterson, C.E. Rice and R.J. Schusterman, eds. The behavior and physiology of pinnipeds. Appleton-Century-Crofts, New York.

Hartman, D.S. 1979. Ecology and behavior of the manatee (*Trichechus manatus*). American Society of Mammalogists, Special Publication No. 5.

Hatakeyama, Y., and H. Soeda. 1990. Studies on echolocation of porpoises taken in salmon gillnet fisheries. Pages 269-281 *in* J.A. Thomas and R.A. Kastelein, eds. Sensory abilities of cetaceans: Laboratory and field evidence. Plenum Press, New York.

Hatakeyama, Y., K. Ishii, T. Akamatsu, H. Soeda, T. Shimamura and T. Kojima. 1994. A review of studies on attempts to reduce the entanglement of the Dall's porpoise, *Phocoenoides dalli*, in the Japanese salmon gillnet fishery. Reports of the International Whaling Commission (Special Issue 15):549-563.

Heffner, R. S., and H.E. Heffner. 1992. Evolution of sound localization in mammals. Pages 691-715 *in* D. Webster, R. Fay and A. Popper, eds. The Biology of Hearing. Springer-Verlag, New York.

Heffner, R. S., and R.B. Masterton. 1990. Sound localization in mammals: Brain-stem mechanisms. Pages 285-314 *in* M.A. Berkley and W.C. Stebbins, eds. Comparative perception. John Wiley and Sons, New York.

Heffner, R.S., and H.E. Heffner. 1980. Hearing in the elephant (*Elephas maximus*). Science 208:518-520.

Henson, O.W., Jr., P.A. Koplas, A.W. Keating, R.F. Huffman and M.M. Henson. 1990. Cochlear resonance in the mustached bat: Behavioral adaptations. Hearing Research 50: 259-274.

Hinchcliffe, R., and A. Pye. 1969. Variations in the middle ear of the Mammalia. Journal of Zoology 157:277-288.

Ingmanson, D.E., and W.J. Wallace. 1973. Oceanology: An introduction. Wadsworth Publishing Co.,Inc., Belmont, Calif.

Jacobs, M. S., P. J. Morgane and W. L. McFarland. 1971. The anatomy of the brain of the bottlenose dolphin (*Tursiops truncatus*). Rhinic lobe (rhinecephalon) I. The paleocortex. Journal of Comparative Neurology 141:205-272.

Jansen, J., and J.K.S. Jansen. 1969. The nervous system of Cetacea Pages 175-252 *in* H.T. Andersen, ed. The biology of marine mammals. Academic Press, New York.

Jensen, F.B., W.A. Kuperman, M.B. Porter, and H. Schmidt. 1994. Computational Ocean Acoustics. AIP Press, New York.

Jewett, D.L. 1970. Volume conducted potentials in response to auditory stimuli as detected by averaging in the cat. Electroencephalography and Clinical Neurophysiology 28:609-618.

Jing Xianying, Y. Xiao and R. Jing. 1981. Acoustic signals and acoustic behaviour of the Chinese river dolphin *Lipotes vexillifer*. Scientica Sinica 24:407-415.

Johnson, C.S. 1968. Masked tonal thresholds in the bottlenosed porpoise. Journal of the Acoustical Society of America 44:965-967.

Johnson, C.S. 1971 Auditory masking of one pure tone by another in the bottlenosed porpoise. Journal of the Acoustical Society of America 49:1317-1318.

Johnson, G. L. 1893. Observations on the refraction and vision of the seal's eye. Proceedings of the Zoological Society of London, No. 48:719-723.

Kamminga C., T. Kataoka and F.J. Engelsma. 1986. Investigations on cetacean sonar VII Underwater sounds of *Neophocaena phocaenoides* of the Japanese coastal populations. Aquatic Mammals 122:52-60.

Kamminga, C. 1988. Echolocation signal types of odontocetes. Pages 9-22 *in* P.E. Nachtigall and P.W.B. Moore, eds. Animal sonar processes and performance. Plenum Press, New York, N.Y.

Kamminga, C., and H. Wiersma. 1981. Investigations on cetacean sonar II. Acoustical similarities and differences in odontocete signals. Aquatic Mammals 82:41-62.

Kamminga, C., and J.G. van Velden. 1987. Investigations on cetacean sonar VIII. Sonar signals of *Pseudorca crassidens* in comparison with *Tursiops truncatus*. Aquatic Mammals 13(2):43-49.

Kamminga, C., M.T. van Hove, F.J. Engelsma and R.P. Terry. 1993. Investigations on cetacean sonar : A comparative analysis of underwater echolocation clicks of *Inia* spp. and *Sotalia* spp. Aquatic Mammals 19(1):31-43.

Kamminga, C.F., F.J. Engelsma and R.P. Terry. 1989. Acoustic observations and comparison on wild, captive and open water *Sotalia* and *Inia*. Page 33 *in* Abstracts of the 8th Biennial Conference on the Biology of Marine Mammals, Pacific Grove, CA.

Kastak, D., and R.J. Schusterman. 1995. Aerial and underwater hearing thresholds for 100Hz pure tones in two pinniped species. Pages 71-81 *in* R.A. Kastelein, J.A. Thomas and P.E. Nachtigall, eds. Sensory systems of aquatic mammals. De Spil Publishers, Woerden, Netherlands.

Kastak, D., and R.J. Schusterman. 1996. Temporary threshold shift in a harbor seal (*Phoca vitulina*). Journal of the Acoustical Society of America 100(3):1905-1908.

Kastelein, R. A. 1991. The relationship between sensory systems and head musculature in the walrus. Page 38 *in* Abstracts of the 9th Biennial Conference on the Biology of Marine Mammals.

Kastelein, R. A., and M. A. vanGaalen. 1988. The sensitivity of the vibrissae of a Pacific walrus (*Odobenus rosmarus divergens*) Part 1. Aquatic Mammals 14:123-133.

Kastelein, R. A., R. C. V. J. Zweypfenning and H. Spekreijse. 1990. Anatomical and histological characteristics of the eyes of a month-old and an adult harbor porpoise (*Phocoena*). Pages 463-480 *in* J. A. Thomas and R. A. Kastelein, eds. Sensory abilities of cetaceans: Laboratory and field evidence. Plenum Press, New York.

Kasuya, T. 1973. Systematic consideration of recent toothed whales based on the morphology of tympano-periotic bone. Scientific Reports of the Whales Research Institute, Tokyo 25:1-103.

Kellogg, W.N. 1959. Auditory perception of submerged objects by porpoises. Journal of the Acoustical Society of America 31:1-6.

Kenyon, K.W. 1981. Sea otter *Enhydra lutris* (Linnaeus, 1758). Pages 209-223 *in* S.H. Ridgway and R.J. Harrison, eds. Handbook of marine mammals, Volume 1: The walrus, sea lions, fur seals and sea otter.

Kerr, A. G., & Byrne, J. E. 1975. Concussive effects of bomb blast on the ear. 89, 131-143.

Ketten, D. R. 1984. Correlations of morphology with frequency for odontocete cochlea: Systematics and topology. Ph. D. dissertation, The Johns Hopkins University, Baltimore, Md. 335 pp.

Ketten, D. R. 1992. The marine mammal ear: Specializations for aquatic audition and echolocation. Pages 717-754 *in* D. Webster, R. Fay and A. Popper, eds. The biology of hearing. Springer-Verlag, New York, NY.

Ketten, D.R. 1993a The Cetacean Ear: Form, frequency, and evolution. In: Marine Mammal Sensory Systems, J. Thomas, R. Kastelein, and A. Supin (eds.), Plenum Press, pp. 53-75.

Ketten, D.R. 1993b Low frequency tuning in marine mammal ears, Symposium on Low Frequency Sound in the Ocean, Tenth Biennial Conference on the Biology of Marine Mammals.

Ketten, D. R. 1994. Functional analyses of whale ears: Adaptations for underwater hearing. I.E.E.E Proceedings in Underwater Acoustics 1:264-270.

Ketten, D.R. 1997. Structure and function in whale ears. Bioacoustics. 103-137.

Ketten, D. R., and D. Wartzok. 1990. Three-dimensional reconstructions of the dolphin cochlea. Pages 81-105 *in* J.A. Thomas and R.A. Kastelein, eds. Sensory abilities of cetaceans: Laboratory and field evidence. Plenum Press, New York.

Ketten, D.R., D.K. Odell and D.P. Domning. 1992. Structure, function, and adaptation of the manatee ear. Pages 77-95 *in* J.A. Thomas, R.A. Kastelein and A.Ya. Supin, eds. Marine mammal sensory systems. Plenum Press, New York, N.Y.

Ketten, D.R., J. Lien, and S. Todd. 1993 Blast injury in humpack whale ears: Evidence and implications, 126th Meeting, Acoustical Society of America, J. Acous. Soc. Am., Vol. 94, no. 3, pt. 2, pp. 1849-1850.

Ketten, D.R., S. Ridgway, and G. Early. 1995. Apocalyptic hearing: Aging, injury, disease, and noise in marine mammal ears. Page 61 *in* Abstracts of the 11th Biennial Conference on the Biology of Marine Mammals.

Kössl, M., and M. Vater 1995. Cochlear structure and function in bats. Pages 191-234 *in* R.R. Fay and A.N. Popper, eds. Hearing by bats. Springer-Verlag, New York, NY.

Kuwada, S.R., R. Batra and V. Maher. 1986. Scalp potentials from normal and hearing impaired subjects in response to SAM tones. Hearing Research 21:179-192.

Ladygina, T. F., V. V. Popov and A. Ya. Supin. 1992. Micromapping of the fur seal's somatosensory cerebral cortex. Pages 107-117 *in* J. A. Thomas, R. A. Kastelein and A. Ya Supin, eds. Marine mammal sensory systems. Plenum Press, New York.

Leatherwood, S., and W.A. Walker. 1979. The northern right whale dolphin *Lissodelphis borealis* Peale in the eastern North Pacific. Pages 85-141 *in* H.E. Winn and B.L. Olla eds. Behavior of marine animals, Volume 3: Cetaceans. Plenum Press, New York.

Leatherwood, S., T.A. Jefferson, J.C. Norris, W.E. Stevens, L.J. Hansen and K.D. Mullin. 1993. Occurrence and sounds of Fraser's dolphins *Lagenodelphis hosei* in the Gulf of Mexico. Texas Journal of Science 45:349-354.

Lehnhardt, E. 1986. Clinical aspects of inner ear deafness. Springer-Verlag, New York, N.Y.

Lende, R. A., and W. I. Welker. 1972. An unusual sensory area in the cerebral neocortex of the bottlenose dolphin, *Tursiops truncatus*. Brain Research 45:555-560.

Levenson, C. 1974. Source level and bistatic target strength of the sperm whale *Physeter catodon* measured from an oceanographic aircraft. Journal of the Acoustical Society of America 55:1100-1103.

Lewis, E.R., E.L. Leverenz and W.S. Bialek. 1985. The Vertebrate inner ear. CRC Press, Inc., Boca Raton, Fla.

Liberman, M. C. 1987 Chronic ultrastructural changes in acoustic trauma: Serial-section reconstruction of stereocilia and cuticular plates, Hearing Research, 26, pp. 65-88.

Lien, J., S. Todd, P. Stevick, F. Marques, and D. Ketten 1993 The reaction of humpback whales to underwater explosions: Orientation, movements, and behavior, 126th Meeting, Acoustical Society of America, J. Acous. Soc. Am., Vol. 94, no. 3, pt. 2, pp. 1849.

Lilly, J.C., and A.M. Miller. 1961. Sounds emitted by the bottlenose dolphin. Science 133:1689-1693.

Lindt, C. C. 1956. Underwater behavior of the Southern sea lion *Otaria jubata*. Journal of Mammalogy 37:287-288.

Lipatov, N.V., and G.N. Solntseva. 1972. Some features of the biomechanics of the middle ear of dolphins. Makhachkala 2:137-140 (read as English summary).

Lipscomb, D.M. 1978. Noise and audiology. University Park Press, Baltimore, MD.

Ljungblad, D.K., S. Leatherwood and M. Dahlheim. 1980. Sounds recorded in the presence of an adult and calf bowhead whale. Marine Fisheries Review 42:86-87.

Long, G.R. 1980. Some psychophysical measurements of frequency in the greater horseshoe bat. Pages 132-135 *in* G. van den Brink and F. Bilsen, eds. Psychophysical, psychological, and behavioral studies in hearing. Delft University Press, Delft.

Lynn, S.K, and D.L. Reiss. 1992. Pulse sequence and whistle production by two captive beaked whales, *Mesoplodon* species. Marine Mammal Science 8:299-305.

Manley, G. A. 1972. A review of some current concepts of the functional evolution of the ear in terrestrial vertebrates. Evolution 26:608-621.

Marsh, H., A.V. Spain and G.E. Heinsohn. 1978. Physiology of the dugong. Comparative Biochemistry and Physiology A 61:159-168.

McCann, T. S. 1982. Aggressive and maternal activities of female southern elephant seals (*Mirounga leonina*). Animal Behavior 30:268-276.

McCormick, J.G., E.G. Wever, G. Palin and S.H. Ridgway. 1970. Sound conduction in the dolphin ear. Journal of the Acoustical Society of America 48:1418-1428.

McCormick, J.G., E.G. Wever, S.H. Ridgway and J. Palin. 1980. Sound reception in the porpoise as it relates to echolocation. Pages 449-467 *in* R.-G. Busnel and J.F. Fish, eds. Animal sonar systems. Plenum Press, New York, N.Y.

McLeod, P.J. 1986. Observations during the stranding of one individual from a pod of pilot whales, *Globicephala malaena*, in Newfoundland. Canadian Field-Naturalist 100:137-139.

Merzenich, M. M., J.H. Kass, M. Sur and C.-S. Lin. 1978. Double representation of the body surface within cytoarchitectonic areas 3b and 1 in "SI" in the owl monkey (*Aotus trivirgatus*). Journal of Comparative Neurology 181:41-74.

Miller, E.H., and D.A. Job. 1992. Airborne acoustic communication in the Hawaiian monk seal, *Monachus schauinslandi*. Pages 485-531 *in* J.A. Thomas, R.A. Kastelein and A.Ya. Supin, eds. Marine mammal sensory systems. Plenum Press, New York, N.Y.

Miller, G.S. 1923. The telescoping of the cetacean skull. Smithsonian Miscellaneous Collection 76:1-67

Møhl, B. 1964. Preliminary studies on hearing in seals. Videnskabelige Meddelelser Fra Dansk Naturhistorisk Forening I Kjobenhaven 127: 283-294.

Møhl, B. 1967. Frequency discrimination in the common seal and a discussion of the concept of upper hearing limit. Pages 43-54 *in* V. Albers, ed. Underwater acoustics. Volume II. Plenum Press, New York, N.Y.

Møhl, B. 1968. Hearing in seals. Pages 172-195 *in* R. Harrison, R. Hubbard, R. Peterson, C. Rice and R. Schusterman, eds. The behavior and physiology of pinnipeds. Appleton-Century, New York, N.Y.

Møhl, B., A. Surlykke and L.A. Miller. 1990. High intensity narwhal clicks. Pages 295-303 *in* J.A. Thomas and R.A Kastelein, eds. Sensory abilities of cetaceans: Laboratory and field evidence. Plenum Press, New York.

Møhl, B., and K. Ronald. 1975. The peripheral auditory system of the harp seal, *Pagophilus groenlandicus* (Erxleben 1777). Rapports et Procés-Verbaux des Réunions, Conseil internationale pour l' exploration de la mer 169:516-523.

Møhl, B., and S. Andersen. 1973. Echolocation: High-frequency component in the click of the harbor porpoise (*Phocoena phocoena* L.)., Journal of the Acoustical Society of America 57:1368-1372.

Møhl, B., J.M. Terhune and K. Ronald. 1975. Underwater calls of the harp seal, *Pagophilus groenlandicus*. Rapports et Procés-Verbaux des Réunions, Conseil internationale pour l' exploration de la mer 169:533-543.

Moore, P.W.B. 1990. Investigations on the control of echolocation pulses in the dolphin. Pages 305-317 *in* J.A. Thomas and R.A. Kastelein, eds. Sensory abilities of cetaceans: Laboratory and field evidence. Plenum Press, New York.

Moore, P.W.B., and R.J. Schusterman. 1976. Discrimination of pure tone intensities by the California sea lion. Journal of the Acoustic Society of America 60:1405-1407.

Moore, P.W.B., and W.W.L. Au. 1975. Underwater localization of pulsed pure tones by the California sea lion *Zalophus californianus*. Journal of the Acoustic Society of America 58:721-727.

Moore, P.W.B., and W.W.L. Au. 1983. Critical ratio and bandwidth of the Atlantic bottlenose dolphin (*Tursiops truncatus*). Journal of the Acoustical Society of America Supplement 1, 74:s73.

Moore, P.W.B., D.A. Pawloski and L. Dankiewicz. 1995. Interaural time and intensity difference thresholds in the bottlenose dolphin (*Tursiops truncatus*). Pages 11-25 *in* R.A. Kastelein, J.A. Thomas and P.E. Nachtigall, eds. Sensory systems of aquatic mammals. DeSpil Publishers, Woerden, Netherlands.

Moore, S.E., and S.H. Ridgway. 1995. Whistles produced by common dolphins from the southern California Bight. Aquatic Mammals 21:55-63.

Moore, S.E., J.K. Francine, A.E. Bowles and J.K.B. Ford. 1988. Analysis of calls of killer whales, *Orcinus orca*, from Iceland and Norway. Rit Fiskideilder 11:225-250.

Morgane, P. J., and J. S. Jacobs. 1972. Comparative anatomy of the cetacean nervous system. Pages 117-224 *in* R. J. Harrison, ed. Functional anatomy of marine mammals. Volume 1. Academic Press, New York.

Morton, A.B., J.C. Gale and R.C. Prince. 1986. Sound and behavioral correlations in captive *Orcinus orca*. Pages 303-333 *in* B.C. Kirkevold and J.S. Lockard, eds. Behavioral biology of killer whales. Alan R. Liss, New York.

Mullin, K.D., L.V. Higgins, T.A. Jefferson and L.J. Hansen. 1994. Sightings of the Clymene dolphin *Stenella clymene* in the Gulf of Mexico. Marine Mammal Science 10:464-470.

Murayama, T., Y. Fujise, I. Aoki and T. Ishii. 1992. Histological characteristics and distribution of ganglion cells in the retinae of the Dall's porpoise and minke whale. Pages 137-145 *in* J. A. Thomas, R. A. Kastelein and A. Ya. Supin, eds. Marine mammal sensory systems. Plenum, New York.

Myrick, A., E. Cassano, C. Oliver, 1989 Potential for physical injury, other than hearing damage, to dolphins from seal bombs in the yellowfin tuna purse-seine fishery: Implications from open-water tests. NMFS report, non-published.

Nachtigall, P. E. 1986. Vision, audition, and chemoreception in dolphins and other marine mammals. Pages 79-113 *in* R. J. Schusterman, J. A. Thomas and F. G. Wood, eds. Dolphin cognition and behavior: A comparative approach. Lawrence Erlbaum Associates, Hillsdale, NJ.

Nachtigall, P.E., W.W.L. Au and J. Pawlowski. 1996. Low-frequency hearing in three species of odontocetes. Journal of the Acoustical Society of America 100:2611.

Nadol, J. B. 1988. Quantification of human spiral ganglion cells by serial section reconstruction and segmental density estimates. American Journal of Otolaryngology 9:47-51.

Nagy, A. R., and K. Ronald. 1970. The harp seal, *Pagophilus groenlandicus* (Erxleben, 1777). VI. Structure of retina. Canadian Journal of Zoology 48:367-370.

Nair, R.V., and R.S. Lal Mohan. 1975. Studies on the vocalisation of the sea cow *Dugong dugong* in captivity. Indian Journal of Fisheries 22:277-278.

Nero, W. 1996. Model Estimates of Acoustic Scattering from Schools of Large Yellowfin Tuna. NRL/SSC report.

NIH/Consensus Development Conference (1990) Noise and Hearing Loss. NIH/CDC, Vol. 8, no. 1. pp. 1-24.

Nishiwaki, M., and H. Marsh. 1985. Dugong *Dugong dugon* (Miller, 1776). Pages 1-31 *in* S.H. Ridgway and R. Harrison, eds. Handbook of marine mammals, Vol 3. Academic Press, London.

Norris , K.S., G.W. Harvey, L.A. Burzell and D.K. Krishna Kartha. 1972. Sound production in the freshwater porpoise *Sotalia* cf. *fluviatilis* Gervais and Deville and *Inia geoffrensis* Blainville in the Rio Negro Brazil. Investigations on Cetacea, G. Pilleri 4:251-262.

Norris, J., and K. Leatherwood. 1981. Hearing in the Bowhead Whale, *Balaena mysticetus*, as estimated by cochlear morphology. Hubbs Sea World Research Institute Technical Report No. 81-132:15.1-15.49.

Norris, K. S. 1968. The evolution of acoustic mechanisms in odontocete cetaceans. Pages 297-324 *in* E.T. Drake, ed. Evolution and environment. Yale University Press, New Haven.
Norris, K. S. 1969. The echolocation of marine mammals Pages 391-423 *in* H.J. Andersen, ed. The biology of marine mammals. Academic Press, New York.
Norris, K.S. 1980. Peripheral sound processing in odontocetes. Pages 495-509 *in* R.-G. Busnel and J.F. Fish, eds. Animal Sonar Systems, Plenum Press, New York.
Norris, K.S., and W.E. Evans. 1967. Directionality of echolocation clicks in the rough-tooth porpoise, *Steno bredanensis* (Lesson). Pages 305-316 *in* W. N. Tavolga, ed. Marine bio-acoustics, Volume 2. Pergamon Press, Oxford.
Norris, K.S., and G.W. Harvey. 1974. Sound transmission in the porpoise head. Journal of the Acoustical Society of America 56:659-664.
Norris, K.S., and W.A. Watkins. 1971. Underwater sounds of *Arctocephalus philippii*, the Juan Fernandez fur seal. Antarctic Research Series 18:169-171.
Norris, K.S., B. Würsig, R.S. Wells and M. Würsig, with S.M. Brownlee, C.M. Johnson and J. Solow. 1994. The Hawaiian spinner dolphin. University of California Press, Berkeley.
Norris, K.S., J.H. Prescott, P.V. Asa-Dorian and P. Perkins. 1961. An experimental demonstration of echolocation behavior in the porpoise, *Tursiops truncatus*, Montagu, Biological Bulletin 120:163-176.
Noseworthy, E., D. Renouf and W.K. Jacobs. 1989. Acoustic breeding displays of harbour seals. Page 46 *in* Abstracts of the 8th Biennial Conference on the Biology of Marine Mammals. Pacific Grove, CA.
Nowak, R.M. 1991. Mammals of the World. Volume 2, 5th edition. The Johns Hopkins University Press, Baltimore, Md.
Odell, D. K., D.J. Forrester and E.D. Asper. 1981. A preliminary analysis of organ weights and sexual maturity in the West Indian manatee (*Trichechus manatus*). Pages 52-65 *in* R.L. Brownell and K. Ralls, eds. The West Indian manatee in Florida. Proceedings of a workshop held in Orlando Florida. PUB, LOC
Oelschläger, H. A. 1986. Comparative morphology and evolution of the otic region in toothed whales Cetacea Mammalia. American Journal of Anatomy 177:353-368.
Oliver, G. W. 1978. Navigation in mazes by a grey seal, *Halichoerus grypus* (Fabricius). Behaviour 67:97-114.
Patterson, J. J. H. 1991. Effects of peak pressure and energy of impulses. 90, 205-208.
Patton, G. W., and E. Gerstein. 1992, Toward understanding mammalian hearing tractability: Preliminary acoustical perception thresholds in the West Indian manatee, *Trichechus manatus*. Page 783 *in* D. Webster, R. Fay and A. Popper, eds. The biology of hearing, Springer-Verlag, Berlin.
Payne, K.B., P. Tyack and R.S. Payne. 1983. Progressive changes in the songs of humpback whales (*Megaptera novaeangliae*). Pages 9-57 *in* R.S. Payne, ed. Communication and behavior of whales. AAAS Selected Symposium Series, Westview Press, Boulder CO.
Payne, K.B., W.J. Langbauer, Jr., and E.M. Thomas. 1986. Infrasonic calls of the Asian elephant (*Elephas maximus*). Behavioral Ecology and Sociobiology 18:297-301.
Phillips, Y., V. Hoyt, T. Mundie, and K. Dodd. 1989 Middle Ear injury in animals exposed to complex blast waves inside an armored vehicle, Ann. Otol. Rhinol. Laryngol., 98: 17-22.
Pickles, J.O. 1982. An introduction to the physiology of hearing. Academic Press, London.
Piggins, D. J. 1970. The refraction of the harp seal, *Pagophilus groenlandicus* (Erxleben 1977). Nature 227:78-79.
Pilleri, G. 1983. The sonar system of the dolphins. Endeavour (New Series) 7(2):59-64.
Pilleri, G. K., K. Zbinden and C. Kraus. 1980. Characteristics of the sonar system of cetaceans with pterygoschisis. Directional properties of the sonar clicks of *Neophocaena phocaenoides* and *Phocoena phocoena* (Phocoenidae). Investigations on Cetacea 11:157-188.
Pilleri, G., and M. Gihr. 1970. The central nervous system of the Mysticete and Odontocete whales. Investigations on Cetacea 2:89-127.
Pilleri, G.C., C. Kraus and M. Gihr. 1971. Physical analysis of the sounds emitted by *Platanista indi*. Investigations on Cetacea 3:22-30.

Pollack, G.D. 1980. Organizational and encoding features of single neurons in the inferior colliculus of bats. Pages 549-587 *in* R.-G. Busnel and J.F. Fish, eds. Animal sonar systems, Plenum Press, New York.

Popov, V.V., and A.Y. Supin. 1990a. Electrophysiological studies on hearing in some cetaceans and a manatee. Pages 405-416 *in* J.A. Thomas and R.A. Kastelein, eds. Sensory abilities of cetaceans: Laboratory and field evidence. Plenum Press, York.

Popov, V.V., and A.Y. Supin. 1990b. Localization of the acoustic window at the dolphin's head. Pages 417-427 *in* J.A. Thomas and R.A. Kastelein, eds. Sensory abilities of cetaceans: Laboratory and field evidence. Plenum Press, New York.

Popov, V.V., T.F. Ladygina and A.Ya. Supin. 1986. Evoked potentials of the auditory cortex of the porpoise *Phocoena phocoena*. Journal of Comparative Physiology 158:705-711.

Popper, A. N. 1980. Sound emission and detection by delphinids. Pages 1-52 *in* L.M. Herman, ed. Cetacean behavior: Mechanisms and functions. John Wiley and Sons, New York.

Poulter, T.C. 1968. Underwater vocalization and behavior of pinnipeds. Pages 69-84 *in* R.J. Harrison, R.C. Hubbard, R.S. Peterson, C.E. Rice and R.J. Schusterman, eds. The behavior and physiology of pinnipeds. Appleton-Century-Crafts, New York.

Pryor, T., K. Pryor and K.S. Norris. 1965. Observations on a pygmy killer whale *Feresa attenuata* Gray from Hawaii. Journal of Mammology 46:450-461.

Pye, A. 1972. Variations in the structure of the ear in different mammalian species. Sound 6:14-18.

Ralls, K.P., P. Fiorelli, and S. Gish. 1985. Vocalizations and vocal mimicry in captive harbor seals, *Pboca vitulina*. Canadian Journal of Zoology 63:1050-1056.

Ramprashad, F., S. Corey and K. Ronald. 1972. Anatomy of the seal ear *Pagophilus groenlandicus* (Erxleben1777). Pages 264-306 *in* R. Harrison, ed. Functional anatomy of marine mammals. Volume I. Academic Press, London.

Ray, G.C. and W.A. Watkins and J.J. Burns. 1969. The underwater song of *Erignathus* (bearded seal), Zoologica 54:79-83, 3 plates, 1 phonograph record.

Ray, G.C., and W.A. Watkins. 1975. Social function of underwater sounds in the walrus *Odobenus rosmarus*. Rapports et Procés-Verbaux des Réunions, Conseil internationale pour l' exploration de la mer 169:524-526.

Rees, D. 1996. Modeling of Acoustic Detection of Yellowfin Tuna in the Eastern Tropical Pacific Fishery Area. (NCCOSC/RDT&E c/541)

Renaud, D.L. and A.N. Popper. 1975. Sound localization by the bottlenose porpoise *Tursiops truncatus*. Journal of Experimental Biology 63:569-585.

Renouf, D. 1992. Sensory reception and processing in Phocidae and Otariidae. Pages 345-394 *in* D. Renouf, ed., Behaviour of pinnipeds. Chapman and Hall, London.

Renouf, D., G. Galway and L. Gaborko. 1980. Evidence for echolocation in harbour seals. Journal of the Marine Biology Association 60:1039-1042.

Repenning, C. 1972. Underwater hearing in seals. Pages 307-331 *in* R. Harrison, ed. Functional anatomy of marine mammals, Volume I. Academic Press, London.

Reysenbach de Haan, F.W. 1956. Hearing in whales, Acta Otolaryngologica Supplement 134:1-114.

Richardson, W.J., C.R. Greene, Jr., C.I. Malme and D.H. Thomson. 1991. Effects of noise on marine mammals. USDI/MMA/OCS study 90-0093. LGL Ecological Research Association. Bryan, Texas.

Richardson, W.J., C.R. Greene, Jr., C.I. Malme and D.H. Thomson. 1995. Marine mammals and noise. Academic Press, New York, N.Y.

Richmond, D., E. Fletcher, J. Yelverton, and Y. Phillips. 1989. Physical Correlates of Eardrum Rupture, Ann. Otol. Rhinol. Laryngol., 98: 35-41.

Ridgway, S. and D. Carder. 1990 Sounds made by a neonatal sperm whale, 120th Meeting, Acoustical Society of America, J. Acous. Soc. Am., Vol. 88, Suppl. 1, p. s6.

Ridgway, S.H. 1972. Mammals of the sea: Biology and medicine. Charles H. Thomas, Springfield, IL.

Ridgway, S.H., T.H. Bullock, D.A. Carder, R.L. Seeley, D. Woods and R. Galambos. 1981. Auditory brainstem response in dolphins, Proceedings of the National Academy of Science 78:1943-1947.

Roberto, M. R. Hamernik, G. Turrentine. 1989. Damage of the auditory system associated with acute blast trauma. Ann. Otol. Rhinol. Laryngol. suppl., 140: 23-34.

Robineau, D. 1969. Morphologie externe du complexe osseux temporal chez les sireniens. Mémoires. du Musée Nationale d'Histoire Naturelle, Nouvelle Séries, Série A, Zoologie 60:1-32.

Rogers, T., D.H. Cato and M.M. Bryden. 1995. Underwater vocal repertoire of the leopard seal *Hydrurga leptonyx* in Prydz Bay, Antarctica *in* R.A. Kastelein, J.A. Thomas and P.E. Nachtigall, eds. Sensory systems of aquatic mammals De Spil Publishers, Woerden, Netherlands.

Rosowski. 1994. Outer and Middle Ears. Pages 172-247 *in* R.R. Fay and A.N. Popper, eds. Comparative hearing: mammals. Springer-Verlag, New York, N.Y.

Sales, G., and D. Pye. 1974. Ultrasonic communication by animals. John Wiley and Sons, New York, N.Y.

Santoro, A.K, K.L. Marten and T.W. Cranford. 1989. Pygmy sperm whale sounds *Kogia breviceps*. Pages 59 *in* Abstracts of the 8th Biennial Conference on the Biology of Marine Mammals. Pacific Grove, CA.

Schevill, W. E, and W.A. Watkins, W. A. 1965. Underwater calls of *Trichechus* (manatee). Nature 205:373-374.

Schevill, W. E. 1964. Underwater sounds of cetaceans. Pages 307-316 *in* W,N, Tavolga, ed. Marine Bio-Acoustics. Pergamon Press, New York.

Schevill, W.E. and W.A. Watkins. 1972. Intense low frequency sounds from an Antarctic minke whale, *Balaenoptera acutorostrata*. Breviora 388:1-8.

Schevill, W.E., and B. Lawrence. 1949. Underwater listening to the white porpoise *Delphinapterus leucas*. Science 109:143-144.

Schevill, W.E., and W.A. Watkins. 1966. Sound structure and directionality in *Orcinus* (killer whale). Zoologica 51:71-76.

Schevill, W.E., and W.A. Watkins. 1971. Pulsed sounds of the porpoise *Lagenorhynchus australis* Breviora 366:1-10.

Schevill, W.E., W.A. Watkins and C. Ray. 1963. Underwater sounds of pinnipeds. Science 141:50-53.

Schevill, W.E., W.A. Watkins, and C. Ray. 1966. Analysis of underwater *Odobenus* calls with remarks on the development and function of the pharyngeal pouches. Zoologica 51(10):103-106.

Schevill, W.E., W.A. Watkins, and C. Ray. 1969. Click structure in the porpoise, *Phocoena phocoena*. Journal of Mammalogy 50:721-728.

Schnitzler, H.U. 1983. Fluttering target detection in horse-shoe bats. Journal of the Acoustical Society of America 74(Supplement 1): S31-S32.

Schuknecht, H.F. 1993. Pathology of the ear, 2nd edition, Lea and Febiger, Philadelphia, Penn.

Schuknecht, H.F., and A.J. Gulya. 1986. Anatomy of the temporal bone with surgical implications. Lea and Feibiger, Philadelphia.

Schultz, K.W., and P.J. Corkeron, 1994. Interspecific differences in whistles produced by inshore dolphins in Moreton Bay, Queensland, Australia. Canadian Journal of Zoology 72:1061-1068.

Schultz, K.W., D.H. Cato, P.J. Corkeron and M.M. Bryden. in press. Low frequency narrow-band sounds produced by bottlenose dolphins. Marine Mammal Science.

Schusterman, R. J. 1981. Behavioral capabilities of seals and sea lions: A review of their hearing, visual, learning and diving skills. Psychological Record 31:125-143.

Schusterman, R., and P.W.B. Moore. 1978a. Underwater audiogram of the northern fur seal *Callorhinus ursinus*. Journal of the Acoustic Society of America 64: S87.

Schusterman, R., and P.W.B. Moore. 1978b. The upper hearing limit of underwater auditory frequency discrimination in the California sea lion. Journal of the Acoustic Society of America 63:1591-1595.

Schusterman, R., R. Balliet, and J. Nixon. 1972. Underwater audiogram of the California sea lion by the conditioned vocalization technique. Journal of Experimental Animal Behaviour 17:339-350.

Schusterman, R.J., R. Gentry and J. Schmook. 1967. Underwater sound production by captive California sea lions, *Zalophus californianus*. Zoologica 52:21-24, 5 plates.

Semmes, J., and L. Porter. 1972. A comparison of precentral and postcentral cortical lesions on somatosensory discrimination in the monkey. Cortex 10:55-68.

Shaw, N.A. 1990. Central auditory conduction time in the rat. Experimental Brain Research 79:217-220.

Shipley, C., B.S. Stewart, and J. Bass. 1992. Seismic communication in northern elephant seals. Pages 553-562 *in* J.A. Thomas, R.A. Kastelein and A.Ya. Supin, eds. Marine mammal sensory systems. Plenum Press, New York, N.Y.

Shochi, Y., K. Zbinden, C. Kraus, M. Gihr and G. Pilleri. 1982. Characteristics and directional properties of the sonar signals emitted by the captive Commerson's dolphin, *Cephalorhynchus commersoni* (Gray, 1846). Investigations on Cetacea 13:177-201.

Silber, G.K. 1986. The relationships of social vocalizations to surface behavior and aggression in the Hawaiian humpback whale (*Megaptera novaeangliae*). Canadian Journal of Zoology 64:2075-2080.

Silber, G.K. 1991. Acoustic signals of the vaquita *Phocoena sinus*. Aquatic Mammals 17(3):130-133.

Simmons, J.A. 1973. The resolution of target range by echolocating bats. Journal of the Acoustical Society of America 54:157-173.

Sjare, B.L., and T.G. Smith. 1986a. The vocal repertoire of white whales, *Delphinapterus leucas*, summering in Cunningham Inlet, Northwest Territories. Canadian Journal of Zoology 64:407-415.

Sjare, B.L., and T.G. Smith. 1986b. The relationship between behavioral activity and underwater vocalizations of the white whale, *Delphinapterus leucas*. Canadian Journal of Zoology 64:2824-2831.

Slip, D. J., M. A. Hindell and H. R. Burton. 1994. Diving behavior of southern elephant seals from Macquarie Island: An overview. Pages 253-270 *in* B. J. Le Boeuf and R. M. Laws, eds. Elephant seals: Population ecology, behavior, and physiology. University of California Press, Berkeley, CA.

Smith, P.F., and J. Wojtowicz. 1985. Temporary auditory threshold shifts induced by twenty-five minute continuous exposures to intense tones in water. Naval Medical Research and Development Command. USN, Report. 1063:1-13.

Smith, P.F., J. Wojtowicz and S. Carpenter. 1988. Temporary auditory threshold shifts induced by ten-minute exposures to continuos tones in water. Naval Medical Research and Development Command. USN, Report 1122:1-10.

Solntseva, G. N. 1971. Comparative anatomical and histological characteristics of the structure of the external and inner ear of some dolphins. Tr. Atl. Nauchno Issled Inst. Rybn. Khoz. Okeanogr. (read as English summary).

Solntseva, G. N. 1990. Formation of an adaptive structure of the peripheral part of the auditory analyzer in aquatic, echo-locating mammals during ontogenesis. Pages 363-384 *in* J.A. Thomas and R.A. Kastelein, eds. Sensory abilities of cetaceans: Laboratory and field evidence. Plenum Press, New York, N.Y.

Sonafrank, N., R. Elsner and D. Wartzok. 1983. The use of acoustic cues in under-ice navigation by a spotted seal (*Phoca largha*). Proceedings of the AAAS Alaska Science Conference.

Sonoda, S. and A. Takemura. 1973. Underwater Sounds of the manatees, *Trichechus manatus manatus* and *T inunguis* (Trichechidae). Report of the Institute for Breeding Research, Tokyo University for Agriculture. 4:19-24.

Spector, W.S. 1956. Handbook of biological data. Saunders, Philadelphia, Penn.
Steiner, W.W. 1981. Species-specific differences in pure tonal whistle vocalizations of five western North Atlantic dolphin species. Behavioral Ecology and Sociobiology 9:241-246.
Steiner, W.W., J.H. Hain, H.E. Winn and P.J. Perkins. 1979. Vocalizations and feeding behavior of the killer whale *Orcinus orcas*. Journal of Mammology 60:823-827.
Stirling, I. 1973. Vocalization in the ringed seal *Phoca hispida*. Journal of the Fisheries Research Board of Canada 30:1592-1594.
Stirling, I., and D.B. Siniff. 1979. Underwater vocalizations of leopard seals *Hydrurga leptonyx* and crabeater seals *Lobodon carcinophagus* near the South Shetland lslands, Antarctica. Canadian Journal of Zoology 57:1244-1248.
Stirling, I., W. Calvert and H. Cleator. 1983. Underwater vocalizations as a tool for studying the distribution and relative abundance of wintering pinnipeds in the high Arctic. Arctic 36:262-274.
Stone, J. 1965. A quantitative analysis of the distribution of ganglion cells in the cat's retina. Journal of Comparative Neurology 124:337-352.
Suga, N. 1983. Neural representation of bisonar (sic) information in the auditory cortex of the mustached bat. Journal of the Acoustical Society of America 74(Supplement 1):S31.
Supin, A.Y., and V.V Popov. 1990. Frequency selectivity of the auditory system of the bottlenosed dolphin *Tursiops truncatus* Pages 385-393. *in* J.A. Thomas and R.A. Kastelein, eds. Sensory abilities of cetaceans: Laboratory and field evidence. Plenum Press, New York, N.Y.
Supin, A.Y., and V.V. Popov. 1993. Direction-dependent spectral sensitivity and interaural spectral difference in a dolphin: Evoked potential study. Journal of the Acoustic Society of America 93:3490-3495.
Taruski, A.G. 1979. The whistle repertoire of the North Atlantic pilot whale *Globicephala malaena* and its relationship to behavior and environment. Pages 345-368 *in* H.E. Winn and B.L. Olla, eds. Behavior of marine animals, Volume 3: Cetaceans. Plenum, New York.
Terhune, J.M. 1994. Geographical variation of harp seal underwater vocalizations. Canadian Journal of Zoology 72:892-897.
Terhune, J.M., and K. Ronald. 1973. Some hooded seal *Cystophora cristata* sounds in March. Canadian Journal of Zoology 51:319-321.
Terhune, J.M., and K. Ronald. 1986. Distant and near-range functions of harp seal underwater calls. Canadian Journal of Zoology 64:1065-1070.
Thomas, J. A., and V.B. Kuechle. 1982. Quantitative analysis of Weddell seal *Leptonychotes weddelli* underwater vocalizations at McMurdo Sound, Antarctica. Journal of the Acoustical Society of America 72:1730-1738.
Thomas, J.A., and C.W. Turl. 1990. Echolocation characteristics and range detection threshold of a false killer whale *Pseudorca crassidens*. Pages 321-334 *in* J.A. Thomas and R.A. Kastelein, eds. Sensory abilities of cetaceans: Laboratory and field evidence. Plenum, New York.
Thomas, J.A., and I. Stirling. 1983. Geographic variation in the underwater vocalizations of Wedell seals *Leptonychotes wedelli* from Palmer Peninsula and McMurdo Sound, Antarctica. Canadian Journal of Zoology 61:2203-2212.
Thomas, J.A., J.L. Pawloski and W.W.L. Au. 1990b. Masked hearing abilities in a false killer whale (*Pseudorca crassidens*). Pages 395-404 *in* J.A. Thomas and R.A. Kastelein, eds. Sensory abilities of cetaceans: Laboratory and field evidence. Plenum Press, New York.
Thomas, J.A., K.C. Zinnel and L.M. Ferm. 1983b. Analysis of Wedell seal *Leptonychotes wedelli* vocalizations using underwater playbacks. Canadian Journal of Zoology 61:1448-1456.
Thomas, J.A., N. Chun and W. Au. 1988. Underwater audiogram of a false killer whale (*Pseudorca crassidens*). Journal of the Acoustical Society of America 84:936-940.
Thomas, J.A., P.W.B. Moore, R. Withrow and M. Stoermer. 1990a. Underwater audiogram of a Hawaiian monk seal *Monachus schauinslandi*. Journal of the Acoustic Society of America 87:417-420.

Thomas, J.A., S.R. Fisher., W.E. Evans and F.T. Awbrey. 1983a. Ultrasonic vocalizations of leopard seals *Hydrurga leptonyx*. Antarctica Journal U.S. 17:186.

Thompson, T.J., H.E. Winn and P.J. Perkins. 1979. Mysticete sounds. Pages 403-431 *in* H.E. Winn and B.L. Olla, eds. Behavior of marine animals, current perspectives in research, Volume 3: Cetaceans. Plenum Press, New York.

Turnbull, S.D., and J.M. Terhune. 1993. Repetition enhances hearing detection thresholds in a harbour seal (*Phoca vitulina*). Canadian Journal of Zoology 71(5):926-932.

Tyack, P. 1985. An optical telemetry device to identify which dolphin produces a sound. Journal of the Acoustical Society of America 7885:1892-1895.

Varanasi, U., and D.G. Malins. 1971. Unique lipids of the porpoise *Tursiops gilli*: Differences in triacyl glycerols and wax esters of acoustic (mandibular canal and melon) and blubber tissues. Biochemica and Biophysica Acta 231:415.

Vater, M. 1988a. Lightmicroscopic observations on cochlear development in horseshoe bats *Rhinolophus rouxii*. Pages 341-345 *in* P.E. Nachtigall and P.W.B. Moore, eds. Animal sonar processes and performance. Plenum Press, New York, N.Y.

Vater, M. 1988b. Cochlear physiology and anatomy in bats. Pages 225-241 *in* P.E. Nachtigall and P.W.B. Moore, eds. Animal sonar processes and performance. Plenum Press, New York, N.Y.

Verboom, W.C., and R.A. Kastelein. 1995. Rutting whistles of a male Pacific walrus (*Odobenus rosmarus divergens*). Pages 287-299 *in* R.A. Kastelein, J.A. Thomas and P.E. Nachtigall, eds. Sensory systems of aquatic mammals. DeSpil Publishers, Woerden, Netherlands.

von Békésy, G. 1960. Experiments in hearing. E.G. Wever (trans.). McGraw-Hill Book Co., Inc., New York, N.Y.

von Uexküll, J.. 1934. A stroll through the worlds of animals and men. A picture book of invisible worlds, translated in *Instinctive Behavior* (1957), Pages 5-80, C. Schiller, ed. London, Metheun.

Voronov, V.A., and I.M. Stosman. 1977. Frequency-threshold characteristics of subcortical elements of the auditory analyzer of the *Phocoena phocoena* porpoise, Zh. Evol.Biokh. I Fiziol., 6:719. (read as English summary)

Wang Ding, B. Würsig and W. Evans. 1995. Comparisons of whistles among seven odontocete species Pages 299-325 *in* R.A. Kastelein, J.A. Thomas and P.E. Nachtigall, eds. Sensory systems of aquatic mammals. De Spil Publishers, Woerden, Netherlands.

Wartzok, D. 1979. Phocid spectral sensitivity curves. Page 62 *in* Proceedings of the 3rd Biennial Conference on the Biology of Marine Mammals, Seattle, Washington.

Wartzok, D., and G. C. Ray. 1976. A verification of Weber's law for visual discrimination of disc sizes in the Bering Sea spotted seal, *Phoca largha*. Vision Research 16:819-822.

Wartzok, D., and M.G. McCormick. 1978. Color discrimination by a Bering Sea spotted seal, *Phoca largha*. Vision Research 18:781-785.

Wartzok, D., R.J. Schusterman and J. Gailey-Phipps. 1984. Seal Echolocation? Nature 308:753.

Wartzok, D., R. Elsner, H. Stone, B.P. Kelly and R.W. Davis. 1992. Under-ice movements and the sensory basis of hole finding by ringed and Weddell seals. Canadian Joural of Zoology 70:1712-1722.

Watkins, W.A. 1967. The harmonic interval: Fact or artifact in spectral analysis of pulse trains. Pages 15-43 *in* W.N. Tavolga, ed. Marine bioacoustics, Volume 2. Pergamon, Oxford, U.K.

Watkins, W.A. 1980. Click sounds from animals at sea. Pages 291-297 *in* R.-G. Busnel and J. F. Fish, eds. Animal sonar systems. Plenum Press, New York.

Watkins, W.A. 1981. The activities and underwater sounds of fin whales. Scientific Reports of the Whales Research Institute 33:83-117.

Watkins, W.A., and G.C. Ray. 1977. Underwater sounds from ribbon seal, *Phoca (Histriophoca) fasciata*. Fisheries Bulletin 75:450-453.

Watkins, W.A., and G.C. Ray. 1985. In-air and underwater sounds of the Ross seal *Ommatophoca rossi*. Journal of the Acoustical Society of America 77:1598-1600.

Watkins, W.A., and W.E. Schevill. 1972. Sound source location by arrival times on a non-rigid three-dimensional hydrophone array. Deep-Sea Research 19:691-706.
Watkins, W.A., and W.E. Schevill. 1974. Listening to Hawaiian spinner porpoises, *Stenella* cf. *longirostris*, with a three-dimensional hydrophone array. Journal of Mammology. 55:319-328.
Watkins, W.A., and W.E. Schevill. 1979. Distinctive characteristics of underwater calls of the harp seal, *Phoca groenlandica*, during the breeding season. Journal of the Acoustical Society of America 66:983-988.
Watkins, W.A., and W.E. Schevill. 1980. Characteristic features of the underwater sounds of *Cephalorhynchus commersonii*. Journal of Mammology 61:738-739.
Watkins, W. A., and D. Wartzok. 1985. Sensory biophysics of marine mammals. Marine Mammal Science 1:219-260.
Watkins, W. A., M. A. Daher, K. M. Fristrup, T. J. Howald and G. N. Di Sciara. 1993. Sperm whales tagged with transponders and tracked underwater by sonar. Marine Mammal Science 9:55-67.
Watkins, W. A., P. Tyack, K.E. Moore and J.E. Bird. 1987. The 20 Hz signals of finback whales, *Balaenoptera physalus*. Journal of the Acoustical Society of America 82:1901-1912.
Watkins, W.A., W.E. Schevill and P.B. Best. 1977. Underwater sounds of *Cephalorhynchus heavisidii* (Mammalia: Cetacea). Journal of Mammology. 58:316-320.
Weast, R.C. 1985. CRC Handbook of Chemistry and Physics, 66th edition. CRC Press, Cleveland, Ohio.
Webster, D. B. 1962. A function of the enlarged middle ear cavities of the Kangaroo rat, *Dipodomys*. American Journal of Anatomy 108:123-148.
Webster, D. B., and M. Webster. 1975. Auditory systems of Heteromyidae: Function, morphology, and evolution of the middle ear. Journal of Morphology 146:343-376.
Webster, D., R. Fay and A. Popper, eds. 1992. The biology of hearing. Springer-Verlag, New York, NY.
West, C.D. 1985. The relationship of the spiral turns of the cochlea and the length of the basilar membrane to the range of audible frequencies in ground dwelling mammals. Journal of the Acoustic Society of America 77:1091-1101.
West, C.D. 1986. Cochlear length, spiral turns and hearing, 12th International Congress on Acoustics 1:B-1.
Wever, E.G., J.G. McCormick, J. Palin and S.H. Ridgway. 1971a. The cochlea of the dolphin, *Tursiops truncatus*: General morphology. Proceedings of the National Academy of Sciences, U.S.A. 68:2381-2385.
Wever, E.G., J.G. McCormick, J. Palin and S.H. Ridgway. 1971b. The cochlea of the dolphin, *Tursiops truncatus:* The basilar membrane. Proceedings of the National Academy of Sciences, U.S.A. 68:2708-2711.
Wever, E.G., J.G. McCormick, J. Palin and S.H. Ridgway. 1971c. The cochlea of the dolphin, *Tursiops truncatus:* Hair cells and ganglion cells. Proceedings of the National Academy of Sciences, U.S.A. 68:2908-2912.
Wever, E.G., J.G. McCormick, J. Palin and S.H. Ridgway. 1972. Cochlear structure in the dolphin, *Lagenorhynchus obliquidens*. Proceedings of the National Academy of Sciences, U.S.A. 69: 657-661.
Winn, H.E., and P.J. Perkins. 1976. Distribution and sounds of the minke whale, with a review of mysticete sounds. Cetology 19:1-12.
Winn, H.E., P.J. Perkins, and L. Winn. 1970. Sounds and behavior of the northern bottle-nosed whale. Pages 53-59 *in* Proceeding of the 7th Annual Conference on Biological Sonar and Diving Mammals. Stanford Research Institute, Menlo Park, Calif.
Wood, F.G., Jr. 1953. Underwater sound production and concurrent behavior of captive porpoises, *Tursiops truncatus* and *Stenella plagiodon*. Bulletin of Marine Science of the Gulf and Caribbean 3:120-133.

Wood, F.G., and W.E. Evans. 1980. Adaptiveness and ecology of echolocation in toothed whales. Pages 381-425 *in* R.-G. Busnel and J.F. Fish, eds. Animal sonar systems, Plenum Press, New York.

Würsig, B., and C. Clark. 1993. Behavior. Pages 157-200 *in* J. Burns, J. Montague, and C. Cowles, eds. The bowhead whale. Society for Marine Mammalogy, Special Publication No. 2, Allen Press, Lawrence, KS.

Xiao Youfu and Jing Rongcai. 1989. Underwater acoustic signals of the baiji, *Lipotes vexillifer*. Pages 129-136 *in* W.F. Perrin, R.L. Brownell, Jr., Zhou Kaiya and Liu Jiankang eds. Biology and conservation of the river dolphins. Occasional Paper. IUCN Species Survival Commission 3. International Union for the Conservation of Nature, Gland, Switzerland.

Yamada, M. 1953. Contribution to the anatomy of the organ of hearing of whales. Scientific Reports of the Whales Research Institute, Tokyo 8:1-79.

Yelverton, J.T. and D. Richmond. 1981 Underwater explosion damage risk criteria for fish, birds, and mammals, J. Acous. Soc. Am., Vol. , 70 (suppl. 1): S84.

Yost, W.A. 1994. Fundamentals of hearing: An introduction, 3rd edition. Academic Press, New York, N.Y.

Zwislocki, J. 1981. Sound analyses in the ear: A history of discoveries. American Scientist 69:184-192.

Table 1. Marine Mammal Sound Production Characteristics

(Data compiled from Popper 1980; Watkins and Wartzok 1985; Richardson *et al.* 1995)

| Scientific Name | Common Name | Signal Type | Frequency Range (kHz) | Frequency near Maximum Energy (kHz) | Source Level (dB re 1 μPa) | References (Partial references only for some species) |
|---|---|---|---|---|---|---|
| **Cetacea** | | | | | | |
| **Odontoceti** | | | | | | |
| **Delphinidae** | | | | | | |
| *Cephalorhynchus commersonii* | Commerson's dolphin | pulsed sounds | <10 | 0.2-5 | - | Watkins and Schevill 1980; Dziedzic and De Buffrenil 1989 |
| | | clicks | - | 6 | - | Dziedzic and De Buffrenil 1989 |
| | | click | 116-134 | - | 160 | Kamminga and Wiersma 1981; Shochi *et al.* 1982; Evans *et al.* 1988; Au 1993 |
| *Cephalorhynchus heavisidii* | Heaviside's dolphin | pulsed sounds | 0.8-5[c] | 0.8-4.5[c] | - | Watkins *et al.* 1977 |
| | | click | 2-51 | - | - | Watkins *et al.* 1977 |
| *Cephalorhynchus hectori* | Hector's dolphin | click | 112-135 | - | 150-163 | Dawson 1988; Dawson and Thorpe 1990; Au 1993 |
| *Delphinus delphis* | Common dolphin | whistles, chirps, barks | - | 2-18 | - | Caldwell and Caldwell 1968; Moore and Ridgway 1995 |
| | | whistles | 4-16 | - | - | Gurevick in Evans 1973 |
| | | click | 0.2-150 | 30-60 | - | Gurevick in Evans 1973 |
| | | click | - | 4-9 | - | Busnel and Dziedzic 1966 |
| | | click | 23-67 | - | - | Dziedzic 1978 |
| *Feresa attenuata* | Pygmy killer whale | growls, blats | - | - | - | Pryor *et al.* 1965 |
| *Globicephala melaena* | Long-finned pilot whale | whistles | 1-8 | 1.6-6.7[a] | - | Busnel and Dziedzic 1966a |
| | | clicks | 1-18 | - | - | Taruski 1979; Steiner 1981 |
| | | click | 6-11 | - | - | McLeod 1986 |
| *Globicephala macrorhynchus* | Short-finned pilot whale | whistles | 0.5->20 | 2-14 | 180 | Caldwell and Caldwell 1969; Fish and Turl 1976 |
| | | click | 30-60 | - | 180 | Evans 1973 |
| *Grampus griseus* | Risso's dolphin | whistles | - | 3.5-4.5 | - | Caldwell *et al.* 1969 |
| | | rasp/pulse burst | 0.1->8 | 2-5 | - | Watkins 1967 |
| | | click | 65 | - | ~120 | Au 1993 |
| *Lagenorhynchus acutus* | Atlantic white-sided dolphin | whistles | - | 6-15[a] | - | Steiner 1981 |
| *Lagenorhynchus albirostris* | White-beaked dolphin | squeals | - | 8-12 | - | Watkins and Schevill 1972 |
| *Lagenorhynchus australis* | Peale's dolphin | pulses (buzz) | 0.3, 4-5 | 0.3 | - | Schevill and Watkins 1971 |
| | | clicks | to 12 | to 5 | low | Schevill and Watkins 1971 |
| *Lagenorhynchus obliquidens* | Pacific white-sided dolphin | whistles | 1->20 | 4-12 | - | Caldwell and Caldwell 1971 |
| | | click | 0.06-80 | 60-80 | 180 | Evans 1973 |
| *Lagenorhynchus obscurus* | Dusky dolphin | whistles | 1.0-27.3 | 6.4-19.2[a] | - | Wang Ding *et al.* 1995 |
| *Lagenodelphis hosei* | Fraser's dolphin | whistles | 7.6-13.4 | - | - | Leatherwood *et al.* 1993 |
| *Lissodelphis borealis* | Northern right whale dolphin | whistles, tones | 1-16 | 1.8, 3 | - | Leatherwood and Walker 1979 |

Table 1 - p. 1

| | | | | | | |
|---|---|---|---|---|---|---|
| *Orcinus orca* | Killer whale | whistles | 1.5-18 | 6-12 | - | Steiner *et al.* 1979; Ford and Fisher 1983; Morton *et al.* 1986 |
| | | click | 0.25-0.5 | - | - | Schevill and Watkins 1966 |
| | | scream | 2 | - | - | Schevill and Watkins 1966 |
| | | click | 0.1-35 | 12-25 | 180 | Dierck *et al.* 1971, Diercks 1972 |
| | | pulsed calls | 0.5-25 | 1-6 | 160 | Schevill and Watkins 1966; Awbrey *et al.* 1982; Ford and Fisher 1983; Moore *et al.* 1988 |
| *Pseudorca crassidens* | False killer whale | whistles | - | 4-9.5 | - | Busnel and Dziedzic 1968; Kamminga and van Velden 1987 |
| | | click | | 25-30; 95-130 | 220-228 | Kamminga and van Velden 1987; Thomas and Turl 1990 |
| *Sotalia fluviatilis* | Tucuxi | whistles | 3.6-23.9 | 7.1-18.5[a] | - | Wang Ding *et al.* 1995 |
| | | click | 80-100 | - | high | Caldwell and Caldwell 1970; Norris *et al.* 1972; Kamminga *et al.* 1993 |
| *Sousa chinensis* | Humpback dolphin | whistles | 1.2->16 | - | - | Schultz and Corkeron 1994 |
| *Stenella attenuata* | Spotted dolphin | whistles | 3.1-21.4 | 6.7-17.8[a] | - | Wang Ding *et al.* 1995 |
| | | whistles | - | - | - | Evans 1967 |
| | | pulse | to 150 | - | - | Diercks 1972 |
| *Stenella clymene* | Clymene dolphin | whistles | 6.3-19.2 | - | - | Mullin *et al.* 1994a |
| *Stenella coeruleoalba* | Spinner dolphin | whistles | 1-22.5 | 6.8-16.9[a] | 109-125 | Watkins and Schevill 1974; Steiner1981; Norris *et al.* 1994; Wang Ding *et al.* 1995 |
| | | pulse bursts | wide band | 5-60 | 108-115 | Watkins and Schevill 1974; Norris *et al.* 1994 |
| | | screams | - | - | - | Norris *et al.* 1994 |
| | | whistles | 6->24 | 8-12.5 | - | Busnel *et al.* 1968 |
| *Stenella frontalis* | Atlantic spotted dolphin | whistles | 5.0-19.8 | 6.7-17.9[a] | - | M.Caldwell *et al.* 1973b; Steiner 1981; Wang Ding *et al.* 1995 |
| | | clicks | 1-8 | - | - | Caldwell and Caldwell 1971a |
| | | squawks, barks, | 0.1-3 | - | - | Caldwell and Caldwell 1971b |
| | | growls,chirps | 4-8 | - | - | Caldwell *et al.* 1973 |
| *Stenella longirostris* | Long-snouted spinner dolphin | | | | - | |
| | | pulse | 1-160 | 5-60 | | Brownlee 1983 |
| | | whistle | 1-20 | 8-12 | - | Brownlee 1983 |
| | | click | low->65 | - | - | Watkins and Schevill 1974; Norris *et al.* 1994 |
| | | click | 1-160 | 60 | - | Ketten 1984 |
| *Steno bredanensis* | Rough-toothed dolphin | whistles | - | 4-7 | - | Busnel and Dziedzic 1966b |
| | | click | 5-32 | - | - | Norris and Evans 1967 |
| *Tursiops truncatus* | Bottlenosed dolphin | whistles | 0.8-24 | 3.5-14.5[a] | 125-173 | Lilly and Miller 1961; Tyack 1985; Caldwell *et al.* 1990; Schultz and Corkeron 1994; Wang Ding *et al.* 1995 |
| | | low frequency narrowband | <2 | 0.3-0.9 | - | Schultz *et al.* in press |
| | | rasp, grate, mew, bark, yelp | - | - | - | Wood 1953 |
| | | click | 0.2-150 | 30-60 | - | Diercks *et al.* 1971 |
| | | bark | 0.2-16 | - | - | Evans 1973 |
| | | whistle | 4-20 | - | - | Evans and Presscott 1962 |
| | | whistle | - | - | - | Caldwell and Caldwell 1967 |
| | | click[d] | 110-130 | - | 218-228 | Au *et al.* 1974; Au 1993 |
| **Monodontidae** | | | | | | |

| | | | | | | |
|---|---|---|---|---|---|---|
| *Delphinapterus leucas* | Beluga | whistles | 0.26-20 | 2-5.9 | - | Schevill and Lawrence 1949; Sjare and Smith 1986a,b |
| | | pulsed tones | 0.4-12 | 1-8 | - | Schevill and Lawrence 1949; Sjare and Smith 1986a,b |
| | | noisy vocalizations | 0.5-16 | 4.2-8.3 | - | Schevill and Lawrence 1949; Sjare and Smith 1986a,b |
| *Monodon monoceros* | Narwhal | echolocation click | | 40-60, 100-120 | 206-225 | Au *et al.* 1985, 1987; Au 1993 |
| | | pulsed tones | 0.5-5 | - | - | Ford and Fisher 1978 |
| | | whistles | 0.3-18 | 0.3-10 | - | Ford and Fisher 1978 |
| | | click | 40 | - | 218 | Møhl *et al.* 1990 |
| **Phocoenidae** | | | | | | |
| *Neophocaena phocaenoides* | Finless porpoise | clicks | 1.6-2.2 | 2 | - | Pilleri *et al.* 1980 |
| *Phocoenoides dalli* | Dall's porpoise | click | 128 | - | - | Kamminga *et al.* 1986; Kamminga 1988 |
| | | clicks | 0.04-12 | - | 120-148 | Evans 1973; Evans and Awbrey 1984 |
| | | click | 135-149 | - | 165-175 | Evans and Awbrey 1984; Hatakeyama and Soeda 1990; Hatakeyma *et al.* 1994 |
| *Phocoena phocoena* | Harbour porpoise | clicks | 2 | - | 100 | Busnel and Dziedzic 1966a; Schevill *et al.* 1969 |
| | | pulse | 100-160 | 110-150 | - | Møhl and Anderson 1973 |
| | | click | 110-150 | - | 135-177 | Busnel *et al.* 1965; Møhl and Anderson 1973; Kamminga and Wiersma 1981; Akamatsu *et al.* 1994 |
| *Phocoena sinus* | Vaquita | click | 128-139 | | - | Silber 1991 |
| **Physeteridae** | | | | | | |
| *Physeter catadon* | Sperm whale | clicks | 0.1-30 | 2-4, 10-16 | 160-180 | Backus and Schevill 1966; Levenson 1974; Watkins 1980 |
| | | coda | 16-30 | - | - | Watkins 1980 |
| *Kogia breviceps* | Pygmy sperm whale | clicks | 60-200 | 120 | - | Santoro *et al.* 1989, Caldwell and Caldwell 1987 |
| **Platanistoidea** | | | | | | |
| **Iniidae** | | | | | | |
| *Inia geoffrensis* | Boutu | squeals | <1->12 | 1-2 | - | Caldwell and Caldwell 1970 |
| | | whistle | 0.2-5.2 | 1.8-3.8[a] | - | Wang Ding *et al.* 1995 |
| | | click | 25-200 | 100 | - | Norris *et al.* 1972 |
| | | | | 95-105 | - | Kaminga, Engelsm and Terry 1989 |
| | | click | 85-105 | | - | Diercks *et al.* 1971; Evans 1973; Kamminga *et al.* 1993 |
| | | click | 20-120 | - | 156 | Xiao Youfu and Jing Rongcai 1989 |
| **Platanistidae** | | | | | | |
| *Platanista minor* | Indus susu | clicks | 0.8-16 | - | low | Andersen and Pilleri 1970 |
| | | click | 15-100 | - | - | Herald *et al.* 1969; Pilleri *et al.* 1971 |
| **Pontoporiidae** | | | | | | |
| *Pontoporia blainvillei* | Franciscana | click | 0.3->24 | - | - | Busnel *et al.* 1974 |
| *Lipotes vexillifer* | Baiji | whistles | 3-18.4 | 6 | 156 | Jing Xianying *et al.* 1981; Xiao Youfu and Jing Rongcai 1989 |
| **Ziphiidae** | | | | | | |
| *Hyperoodon ampullatus* | Northern bottle-nose whale | whistles | 3-16 | - | - | Winn *et al.* 1970 |
| *Hyperoodon spp.* | Bottlenose whale | clicks | 0.5->26 | - | - | Winn *et al.* 1970 |
| | | click | 8-12 | | - | Winn *et al.* 1970 |

| | | | | | | |
|---|---|---|---|---|---|---|
| *Mesoplodon densirostris* | Blainville's beaked whale | short whistles | <1-6 | - | - | Caldwell and Caldwell 1971 |
| *Mesoplodon carlhubbsi* | Hubb's beaked whale | pulses | 0.3-80 | 0.3-2 | - | Buerki *et al.* 1989; Lynn and Reiss 1992 |
| | | whistles | 2.6-10.7 | - | - | Buerki *et al.* 1989; Lynn and Reiss 1992 |
| **Mysticeti** | | | | | | |
| **Balaenidae** | | | | | | |
| *Balaena mysticetus* | Bowhead | calls | .1-0.580 | .14-.16 | 128-190 | Thompson *et al.* 1979; Ljungblad *et al.* 1980; Norris and Leatherwood 1981; Würsig and Clark 1993 |
| *Eubalaena glacialis* | Northern right whale | call | <0.400 | <0.200 | - | Watkins and Schevill 1972; Clark 1990 |
| **Balaenopteridae** | | | | | | |
| *Balaenoptera acutorostrata* | Minke whale | sweeps, moans | 0.06-0.140 | - | 151-175 | Winn and Perkins 1976; Schevill and Watkins 1972 |
| *Balaenoptera musculus* | Blue whale | moans | 0.012-0.40 | 0.012-.018 | 188 | Cummings and Thompson 1971; Edds 1982 |
| *Balaenoptera physalus* | Fin whale | moans | 0.016-0.75 | 0.020 | 160-190 | Thompson *et al.* 1979; Edds 1988 |
| | | pulse | .040-.075 | - | - | Clark 1990 |
| | | pulse | .018-.025 | .020 | - | Watkins 1981 |
| | | ragged pulse | <.030 | - | - | Watkins 1981 |
| | | rumble | - | <.030 | - | Watkins 1981 |
| *Megaptera novaeanglia* | Humpback whale | songs | 0.03-8 | .1-4 | 144-186- | Thompson *et al.* 1979;Watkins 1981; Edds 1982,1988; Payne *et al.* 1983; Silber 1986; Clark 1990; Dahlheim and Ljungblad 1990 |
| | | social | .05-10.0 | <3 | - | Thompson, Winn and Perkins 1979 |
| **Eschrichtiidae** | | | | | | |
| *Eschrictius robustus* | Gray whale | call | 0.2-2.5 | 1-1.5 | - | Dahlheim and Ljungblad 1990 |
| **Fissipedia** | | | | | | |
| **Mustelidae** | | | | | | |
| Enhydra lutris | Sea otter | growls[b] whine | 3-5 | - | - | Kenyon 1981; Richardson *et al.* 1995 |
| **Pinnipedia** | | | | | | |
| **Odobenidae** | | | | | | |
| *Odobenus rosmarus* | Walrus | bell tone | - | 0.4-1.2 | - | Schevill *et al.* 1966; Ray and Watkins 1975; Stirling *et al.* 1983 |
| | | clicks,taps, knmks | 0.1-10 | <2 | - | Schevill *et al.* 1966; Ray and Watkins 1975; Stirling *et al.* 1983 |
| | | rasps | 0.2-0.6 | 0.4-0.6 | - | Schevill *et al.* 1966 |
| | | grunts | ≤1 | ≤1 | - | Stirling *et al.* 1983 |
| **Otariidae** | | | | | | |
| *Arctocephalus philippii* | Juan Fernandez fur seal | clicks | 0.1-0.2 | 0.1-0.2 | - | Norris and Watkins 1971 |
| *Callorhinus ursinus* | Northern fur seal | clicks,bleats | - | - | - | Poulter 1968 |
| *Eumetopias jubatus* | Northern sea lion | clicks,growls | - | - | - | Poulter 1968 |
| *Zalophus californianus* | California sea lion | barks | <8 | <3.5 | - | Schusterman *et al.* 1967 |
| | | whinny | <1-3 | - | - | Schusterman *et al.* 1967 |

Table 1 - p. 4

| | | | | | | |
|---|---|---|---|---|---|---|
| | | clicks | - | 0.5-4 | - | Schusterman *et al.* 1967 |
| | | buzzing | <1-4 | <1 | - | Schusterman *et al.* 1967 |
| **Phocidae** | | | | | | |
| *Cystophora cristata* | Hooded seal | grunt | - | 0.2-0.4 | - | Terhune and Ronald 1973 |
| | | snort | - | 0.1-1 | - | Terhune and Ronald 1973 |
| | | buzz(click) | to 6 | 1.2 | - | Terhune and Ronald 1973 |
| *Erignathus barbatus* | Bearded seal | song | 0.02-6 | 1-2 | 178 | Ray *et al.* 1969; Stirling *et al.* 1983; Cummings *et al.* 1983 |
| *Halichoerus grypus* | Gray seal | clicks, hiss | 0-30, 0-40 | - | - | Schevill *et al.* 1963; Oliver 1978 |
| | | 6 call types | 0.1-5 | 0.1-3 | - | Asselin *et al.* 1993 |
| | | knocks | to 16 | to 10 | - | Asselin *et al.* 1993 |
| *Hydrurga leptonyx* | Leopard seal | pulses and trills | 0.1-5.9 | - | - | Ray 1970; Stirling and Siniff 1979; Rogers *et al.* 1995 |
| | | thump,blast | 0.04-7 | - | - | Rogers *et al.* 1995 |
| | | ultrasonic | up to 164 | 50-60 | low | Thomas *et al.* 1983a |
| *Leptonychotes weddellii* | Weddell seal | >34 call types | 0.1-12.8 | - | 153-193 | Thomas and Kuechle 1982; Thomas *et al.* 1983b; Thomas and Stirling 1983 |
| *Lobodon carcinophagus* | Crabeater seal | groan | <0. 1->8 | 0.1-1.5 | high | Stirling and Siniff 1979 |
| *Ommatophoca rossii* | Ross seal | pulses | 0.25-1 | - | - | Watkins and Ray 1985 |
| | | siren | 4-1-4 | - | - | Watkins and Ray 1985 |
| *Phoca fasciata* | Ribbon seal | frequency sweeps | 0.1-7.1 | - | 160 | Watkins and Ray 1977 |
| *Phoca hispida* | Ringed seal | barks, clicks, yelps | 0.4-16 | <5 | 95-130 | Stirling 1973; Cummings *et al.* 1984 |
| *Phoca largha* | Spotted seal | clicks | 8-150 | 1240 | - | Schevill *et al.* 1963; Cummings and Fish 1971; Renouf *et al.* 1980; Noseworthy *et al.* 1989 |
| | | roar | 0.4-4 | 0.4-0.8 | - | Hanggi and Schusterman 1992, 1994 |
| | | bubbly growl | <0.1-0.4 | <0.1-0.25 | - | Hanggi and Schusterman 1992, 1994 |
| | | grunt, groan | <0.1-4 | - | - | Hanggi and Schusterman 1992, 1994 |
| | | creak | 0.7-4 | 0.7-2 | - | Hanggi and Schusterman 1992, 1994 |
| *Phoca (Pagophilus) groenlandica* | Harp seal | 15 sound types | <0.1->16 | 0.1-3 | 130-140 | Møhl *et al.* 1975; Watkins and Schevill 1979; Terhune and Ronald 1986; Terhune 1994 |
| | | clicks | - | 30 | 131-164 | Møhl *et al.* 1975 |
| *Phoca vitulina* | Harbor seal | social sounds | 0.5-3.5 | - | - | Beier and Wartzok 1979 |
| **Sirenia** | | | | | | |
| **Dugongidae** | | | | | | |
| *Dugong dugon* | Dugong | chirp-squeak[b] | 3-8 | - | low | Nair and Mohan 1975 |
| | | sound 1[b] | 1-2 | - | | Marsh *et al.* 1978 |
| | | chirp[b] | 2-4 | - | - | Marsh *et al.* 1978 |
| | | all sounds | 0.5-18 | 1-8 | | Nishiwaki and Marsh 1985; Anderson and Barclay 195 |
| **Trichechidae** | | | | | | |
| *Trichechus inunguis* | Amazon manatee | squeaks,pulses | 6-16 | 6-16 | - | Evans and Herald 1970 |
| *Trichechus manatus* | West Indian manatee | squeaks | 0.6-16 | 0.6-5 | low | Schevill and Watkins 1965 |

[a]Frequency determined as "mean minimum frequency minus 1 s.d...to...mean maximum frequency plus 1 s.d." (*sensu* Richardson *et al* 1995).
[b]Recorded in air.

Table 1 - p. 5

[c]Equipment capable of recording to 10 kHz only.
[d]Performance in high background noise (Au, 1993)

Table 2. Auditory, Vestibular, and Optic Nerve Distributions
(Data compiled from Yamada 1953; Gacek and Rasmussen 1961; Jansen and Jansen 1969; Firbas 1972; Morgane and Jacobs 1972; Bruns and Schmieszek 1980; Dawson 1980; Ketten 1984, 1992; Vater 1988; Nadol 1988; Gao and Zhou 1991, 1992, 1995; Kössl and Vater 1995).

| Species | Common Name | Cochlear Type | Membrane Length (mm) | Auditory Ganglion Cells | Density (cells/mm cochlea) | Vestibular Ganglion Cells | Vestibular-Auditory Ratio | Optic Nerve Fibers | Optic-Auditory Ratio | Optic-Vestibular Ratio |
|---|---|---|---|---|---|---|---|---|---|---|
| *Inia geoffrensis* | Boutu | I | 38.2 | 104,832 | 2744 | | | 15,500 | 0.15 | |
| *Lipotes vexillifer* | Baiji | | | 82,512 | | 3,605 | 0.04 | 23,800 | 0.29 | 6.60 |
| *Neophocoena phocoenoides* | Finless porpoise | | | 68,198 | | 3,455 | 0.05 | 88,900 | 1.30 | 25.73 |
| *Sousa chinensis* | Humpbacked dolphin | | | 70,226 | | 3,213 | 0.05 | 149,800 | 2.13 | 46.62 |
| *Phocoena phocoena* | Harbour porpoise | I | 22.5 | 70,137 | 3117 | 3,200 | | 81,700 | 1.16 | 25.53 |
| *Delphinapterus leucas* | Beluga | | 42 | 149,386 | 3557 | | | 110,500 | 0.74 | |
| *Delphinus delphis* | Common dolphin | II | 34.9 | 84,175 | 2412 | 4,091 | 0.05 | 165,600 | 1.97 | 40.48 |
| *Lagenorhynchus obliquidens* | White-sided dolphin | II | 34.9 | 70,000 | 2006 | | | 77,500 | 1.11 | |
| *Stenella attenuata* | Spotted dolphin | II | 36.9 | 82,506 | 2236 | | | | | |
| *Tursiops truncatus* | Bottlenosed dolphin | II | 38.9 | 96,716 | 2486 | 3,489 | 0.04 | 162,700 | 1.68 | 46.63 |
| *Physeter catodon* | Sperm Whale | | 54.3 | 161,878 | 2981 | | | 172,000 | 1.06 | |
| *Balaenoptera physalus* | Fin Whale | M | 64.7 | 134,098 | 2073 | | | 252,000 | 1.88 | |
| *Megaptera novaeangliae* | Humpback Whale | M | 58 | 156,374 | 2696 | | | 347,000 | 2.22 | |
| *Rhinolophus ferrumequinum* | Horseshoe bat | T | 16.1 | 15,953 | 991/1750* | | | | | |
| *Pteronotus parnellii* | Mustached bat | T | 14.0 | 12,800 | 900/1900* | | | | | |
| *Cavia porcella* | Guinea Pig | T | 19.0 | 24,011 | 1264 | 8,231 | 0.34 | | | 0.00 |
| *Felis domesticus* | Cat | T | 28.0 | 51,755 | 1848 | 12,376 | 0.24 | 193,000 | 3.73 | 15.59 |
| *Homo sapiens* | Human | T | 32.1 | 30,500 | 950 | 15,590 | 0.51 | 1,159,000 | 38.00 | 74.34 |

*Densities at auditory fovea as described by Bruns and Schmiezek (1980)

Table 3.
(Data compiled from Lipscomb 1978; Lehnhardt 1986; Liberman 1987; Patterson 1991)

| SOURCE | LEVEL (dB) | EXPOSURE TIME | $TTS_{30}$ (dB) | BAND |
|---|---|---|---|---|
| **HUMAN** | | | | |
| narrowband (<10 kHz) | (occupational) | 10 yrs | (20-60) | CF + 1/2 octave |
| 500 Hz | 81.5 | 48 hours | 10.5 | (3 day recovery) |
| 500 Hz | 92.5 | 29.5 hours | 27.5 | (asymptotic loss at 12 hrs.) |
| 500 Hz | 90 | 48 hours | 27.5 | (4 day recovery) |
| **CAT** | | | | |
| broadband noise | 105 | 15 min. | 20-40 | 2-8 kHz |
| broadband noise | 115 | 7.5 min. | 20-50 | 2-8 kHz |
| broadband noise, repeat | 115 | 7.5 min. on 24 hrs off | 20-30 | 3.5 kHz |
| broadband noise, repeat | 115 | 7.5 min. on 1-6 hrs off | 30-50 (some PTS) | 2-8 kHz |
| 500 Hz CF 1 octave band | 105 | 8-48 hours | 20-30 (no PTS) | 2-8 kHz |
| **CHINCHILLA** | | | | |
| 500 Hz CF/1 octave band | (100) | 48 Hrs | 40-45 | 2-8 kHz |
| 500 Hz CF/1 octave band | 100 | 7 days | 60 | 0.75 kHz |
| 500 Hz CF/1 octave band | 75 | 7-21 days | 30-35 | 0.15 - 8 kHz |
| 4 KHz CF/1 octave band | 86-98 | 9 days | 20-35 | 3 - 8 kHz (15 day recovery) |
| **SQUIRREL MONKEY** | | | | |
| 500 Hz CF/1 octave band | 100 | 2 Hrs | 30-40 | 0.5-2 kHz (2 day recovery) |
| 2 kHz CF/1 octave band | 100 | 2 Hrs | 40-50 | 2-6 kHz |
| pure tones | 120 | 9-15 mins. | 16-23 | CF+1/2 octave |

CF - Center Frequency of exposure band

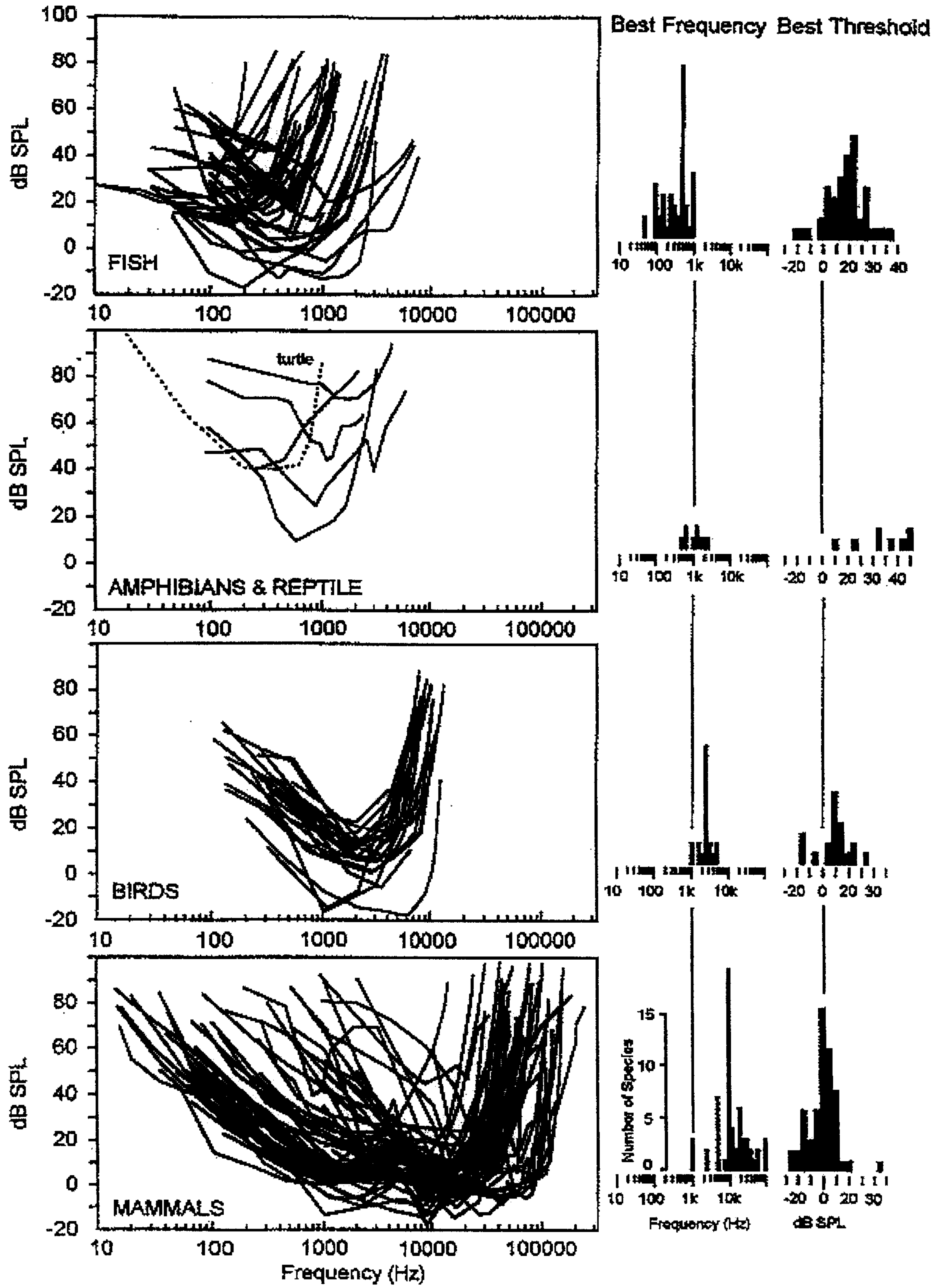


Figure 1. Audiograms of representative terrestrial mammals. Note that the ordinate is labeled dB SPL and that thresholds are therefore at or near 0 dB in the regions of best sensitivity for most species. The histograms to the right of the audiograms show the distribution of peak sensitivities and level at peak for each group. (Data compiled from Fay 1988, Yost, 1994, Yost, ASA Bioacoustic Workshop Materials, MMS Biennial Conf., 1995).

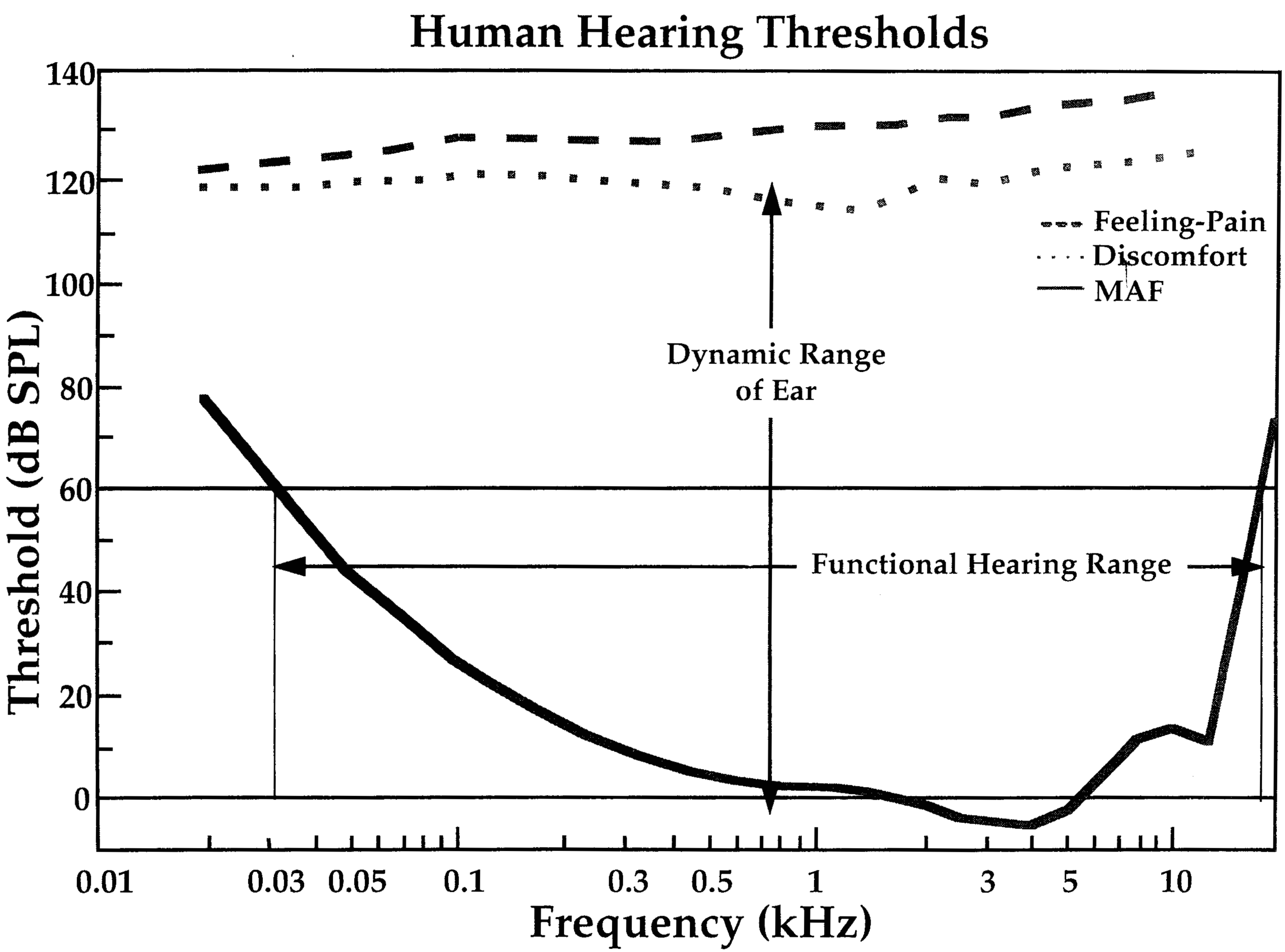


Figure 2. The human audiogram shown represents a minimum audible field (MAF) response for an average adult tested in quiet. This curve can be compared with the audiograms for land mammals in air with the underwater audiograms for cetaceans and pinnipeds in Figure 3, taking into consideration the effect that differing reference pressures have on reported threshold values. A transposition of this curve with some of the marine mammal curves is shown also in Figure 7, but to accomplish this, a conversion of all curves to to watts/m$^2$ was required before they were subsequently replotted for with a common reference pressure of dB re 1 μPa.

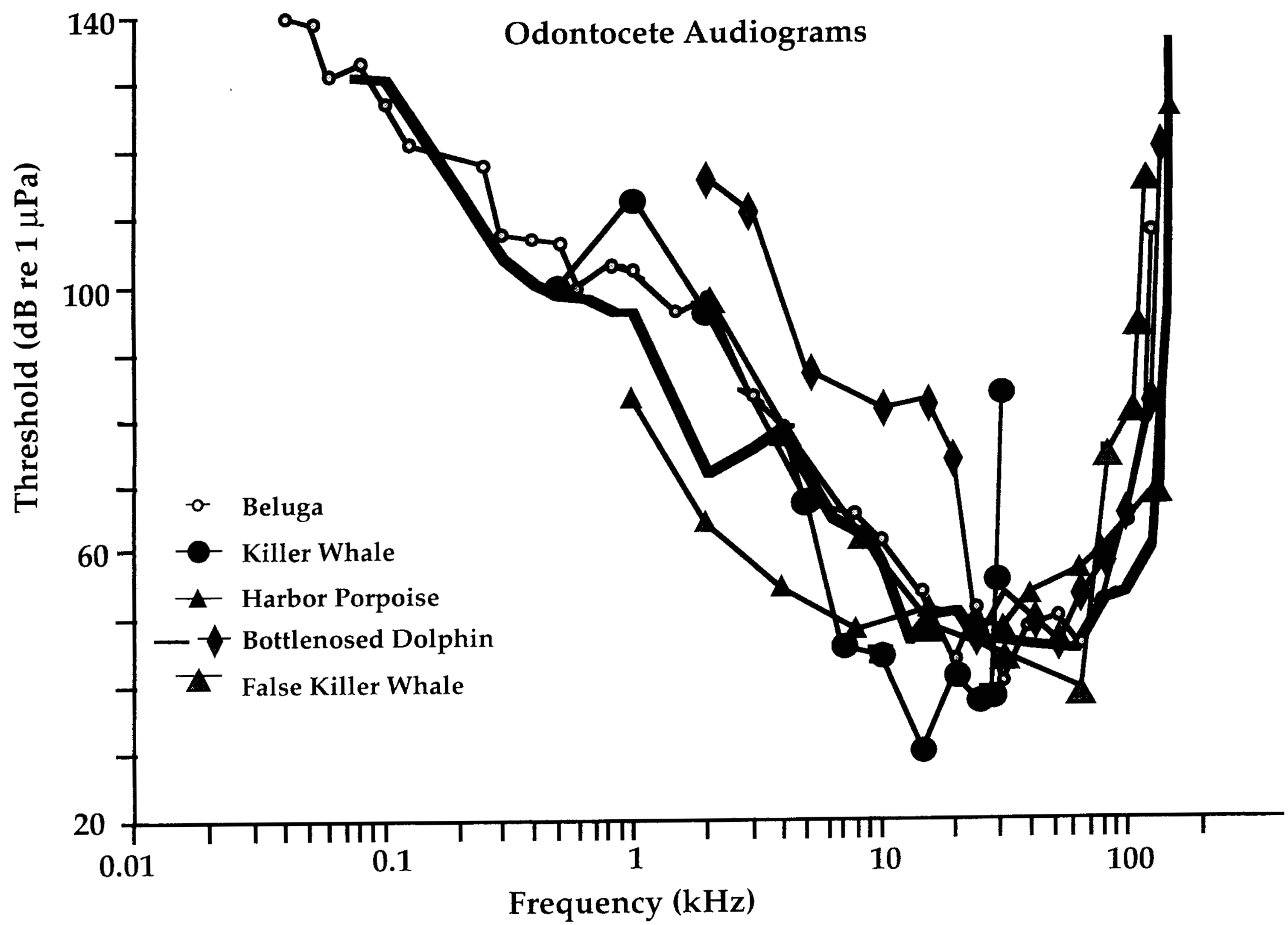


Figure 3. Underwater audiograms for (A) odontocetes and (B) pinnipeds. For some species, more than one curve is shown because data reported in different studies were not consistent. Note that for both the bottlenose dolphin and the sea lion, thresholds are distinctly higher for one of the two animals tested. These differences may reflect different test conditions or a hearing deficit in one of the animals. (Summary data compiled from Popper 1980; Fay 1988; Au 1993; Richardson *et al.* 1995. **Beluga**: White et al. 1978; Awbrey et al. 1988 and Johnson et al. 1989. **Killer Whale**: Hall & Johnson 1971 and Hall & Johnson 1972. **Harbor Porpoise**: Anderson 1970 and Anderson 1970a. **Bottlenose Dolphin**: Johnson 1967 and Ljungblad et al. 1982b. **False Killer Whale**: Thomas et al. 1988a. **California Sea Lion**: Schusterman et al. 1972; Kastak & Schusterman 1995 and Schusterman, Balliet & Nixon 1972. **Northern Fur Seal**: Moore & Schusterman 1987; Babushina et al. 1991 and Schusterman & Moore 1978a. **Harbor Seal**: Mohl 1968; Mohl 1968a; Kastak & Schusterman 1995 and Terhune & Turnbull 1995. **Ringed Seal**: Terhune & Ronald 1975a. **Harp Seal**: Terhune & Ronald 1972. **Monk Seal**: Thomas et al. 1990b.).

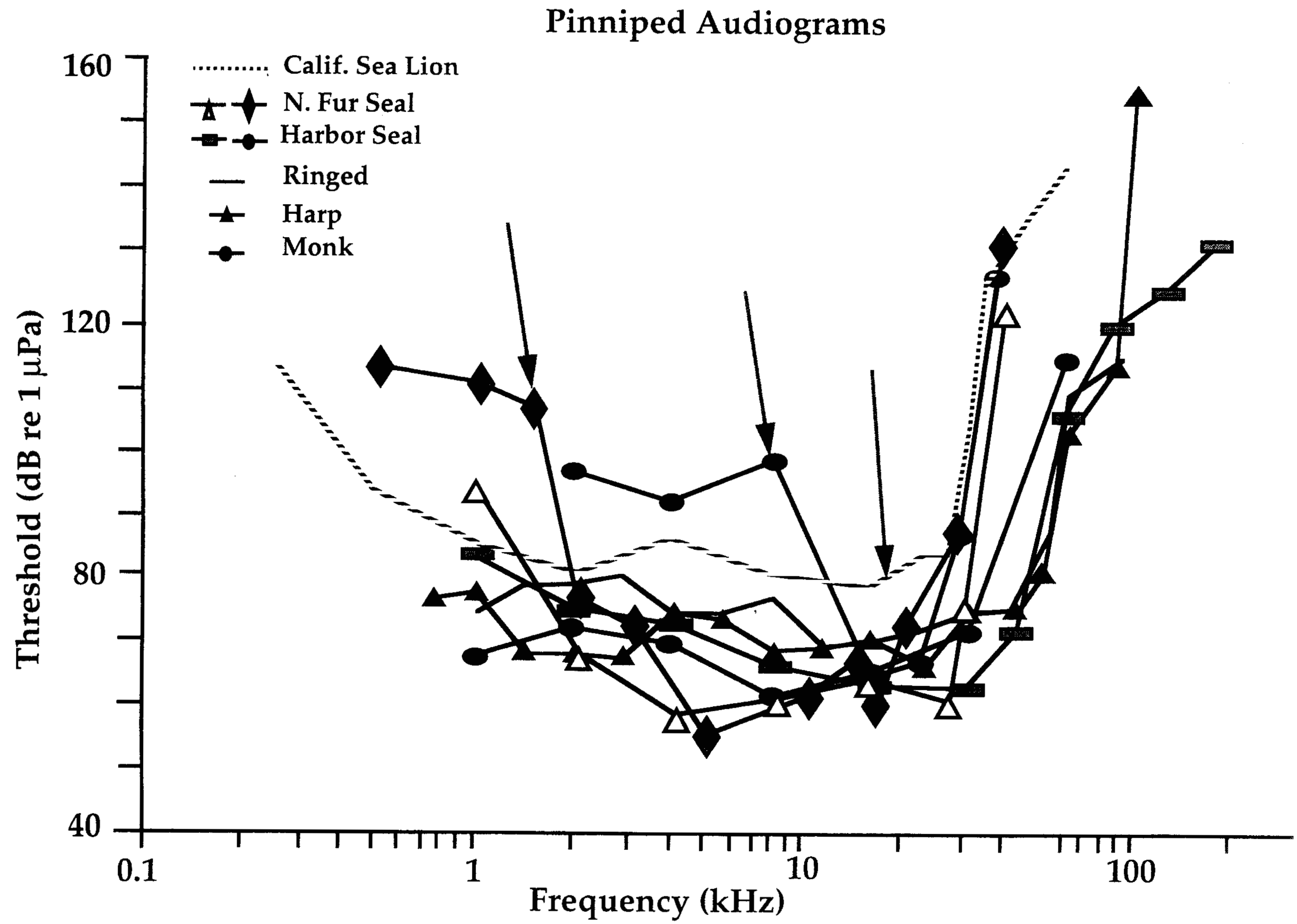


Figure 3. Underwater audiograms for (A) odontocetes and (B) pinnipeds. For some species, more than one curve is shown because data reported in different studies were not consistent. Note that for both the bottlenose dolphin and the sea lion, thresholds are distinctly higher for one of the two animals tested. These differences may reflect different test conditions or a hearing deficit in one of the animals. (Summary data compiled from Popper 1980; Fay 1988; Au 1993; Richardson *et al.* 1995. **Beluga**: White et al. 1978; Awbrey et al. 1988 and Johnson et al. 1989. **Killer Whale**: Hall & Johnson 1971 and Hall & Johnson 1972. **Harbor Porpoise**: Anderson 1970 and Anderson 1970a. **Bottlenose Dolphin**: Johnson 1967 and Ljungblad et al. 1982b. **False Killer Whale**: Thomas et al. 1988a. **California Sea Lion**: Schusterman et al. 1972; Kastak & Schusterman 1995 and Schusterman, Balliet & Nixon 1972. **Northern Fur Seal**: Moore & Schusterman 1987; Babushina et al. 1991 and Schusterman & Moore 1978a. **Harbor Seal**: Mohl 1968; Mohl 1968a; Kastak & Schusterman 1995 and Terhune & Turnbull 1995. **Ringed Seal**: Terhune & Ronald 1975a. **Harp Seal**: Terhune & Ronald 1972. **Monk Seal**: Thomas et al. 1990b.).

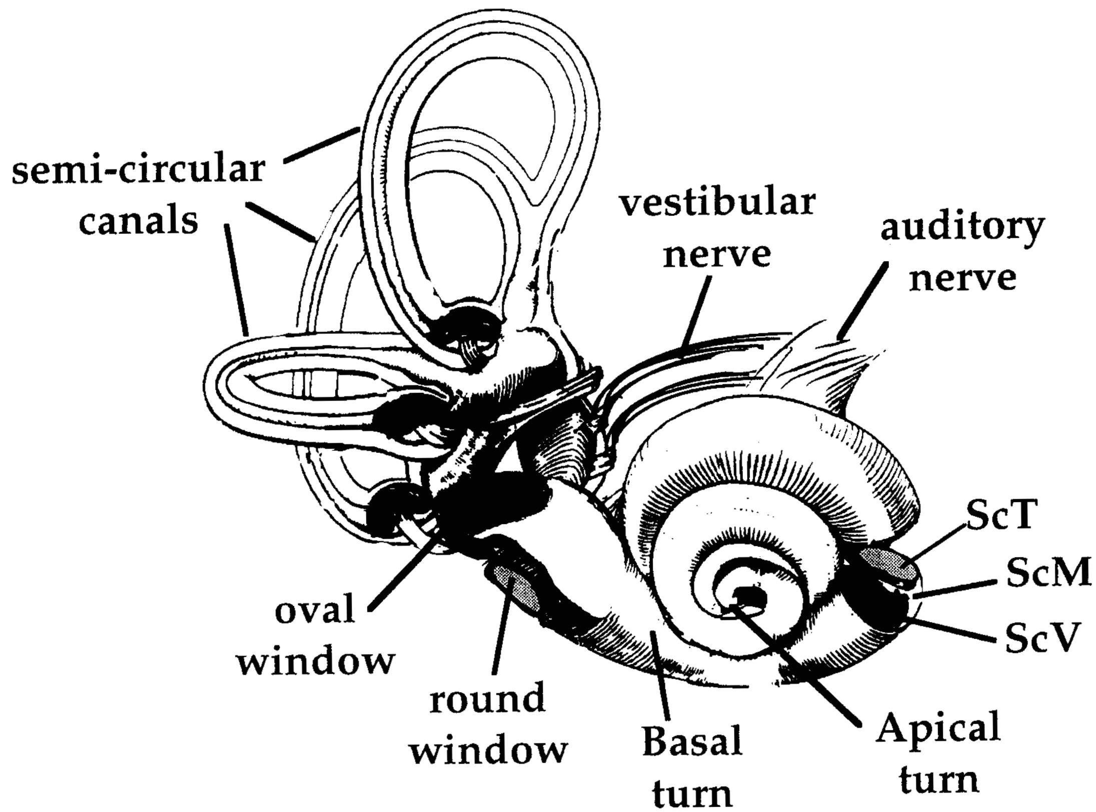


Figure 4A. The two drawings (A and B) illustrate the fundamental structure of a mammalian inner ear. 4a shows an average mammalian 2.5 turn cochlea and 3 semicircular canals. A wedge has been removed from the basal turn to show the three chambers or scalae in the cochlea. ScV scala vestibuli; ScM scala media; ScT scala tympani. A hypothetical mammalian cochlea is "unrolled" in 4b to illustrate changes in basilar membrane width with cochlear length. The broader apical end which responds to low frequencies is in the foreground. A membrane place vs. frequency distribution is shown for this ear's theoretical hearing range with the approximate envelope of membrane displacements for three pure tone sounds. The approximate widths for this membrane would be 100 μ at the base and 400 μ at the apex (Redrawn redrawn from an archive illustration of the Dept. of Otolaryngology, Mass. Eye and Ear Infirmary).

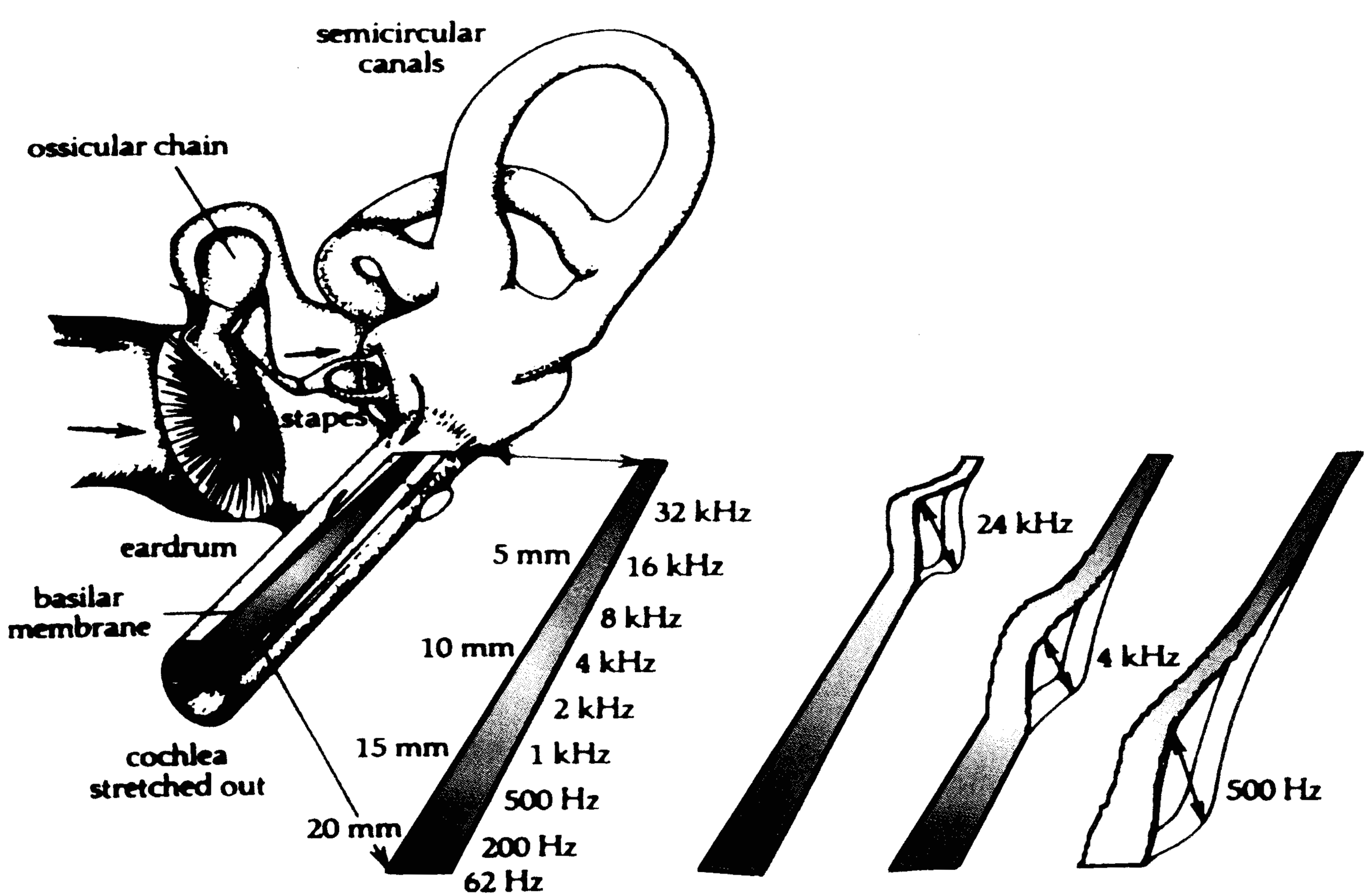


Figure 4B. The two drawings (A and B) illustrate the fundamental structure of a mammalian inner ear. 4a shows an average mammalian 2.5 turn cochlea and 3 semicircular canals. A wedge has been removed from the basal turn to show the three chambers or scalae in the cochlea. ScV scala vestibuli; ScM scala media; ScT scala tympani. A hypothetical mammalian cochlea is "unrolled" in 4b to illustrate changes in basilar membrane width with cochlear length. The broader apical end which responds to low frequencies is in the foreground. A membrane place vs. frequency distribution is shown for this ear's theoretical hearing range with the approximate envelope of membrane displacements for three pure tone sounds. The approximate widths for this membrane would be 100 μ at the base and 400 μ at the apex (Redrawn redrawn from an archive illustration of the Dept. of Otolaryngology, Mass. Eye and Ear Infirmary).

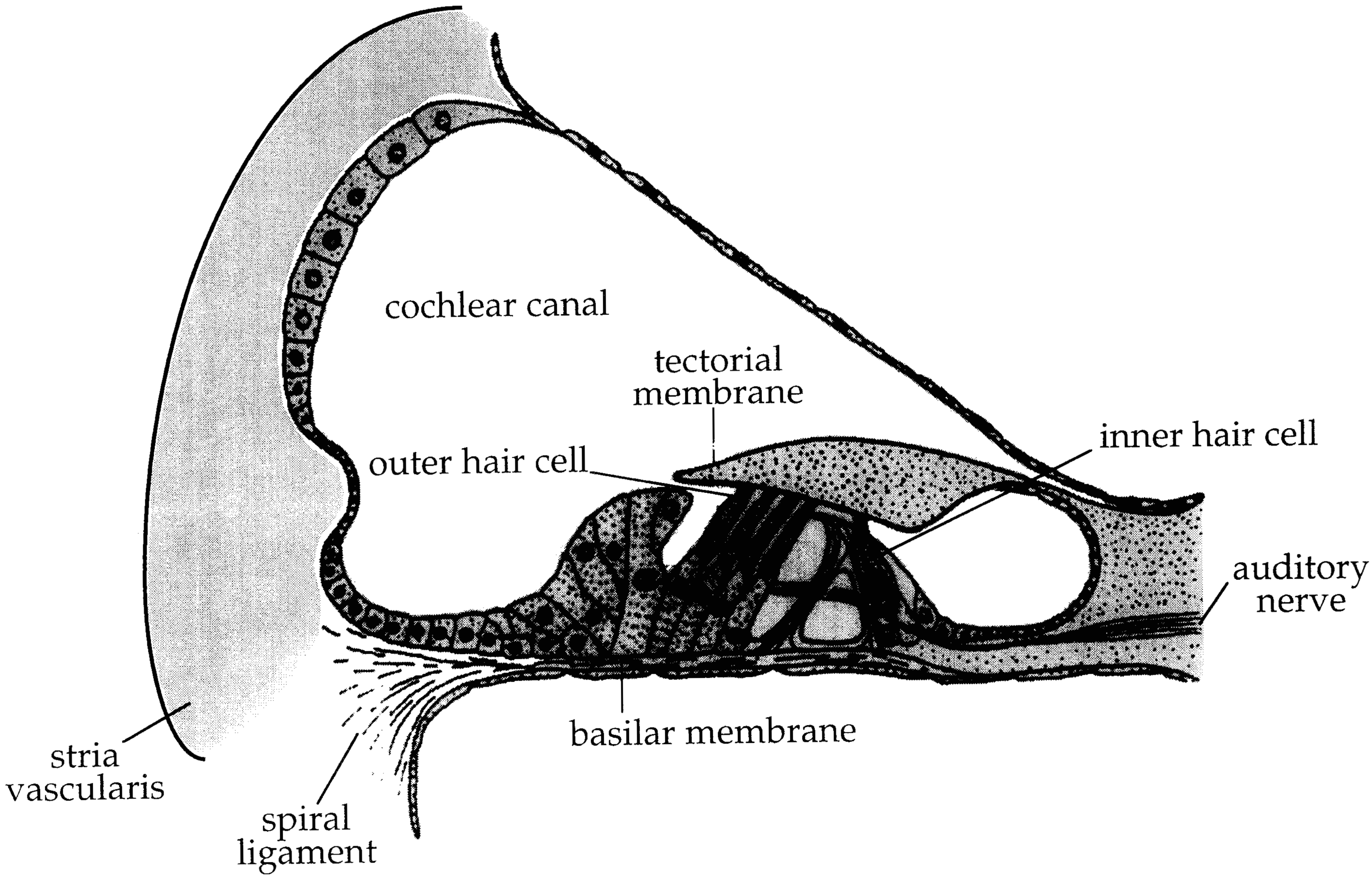


Figure 5. A schematic of the cochlear duct and the Organ of Corti are shown for a generic mammal ear.

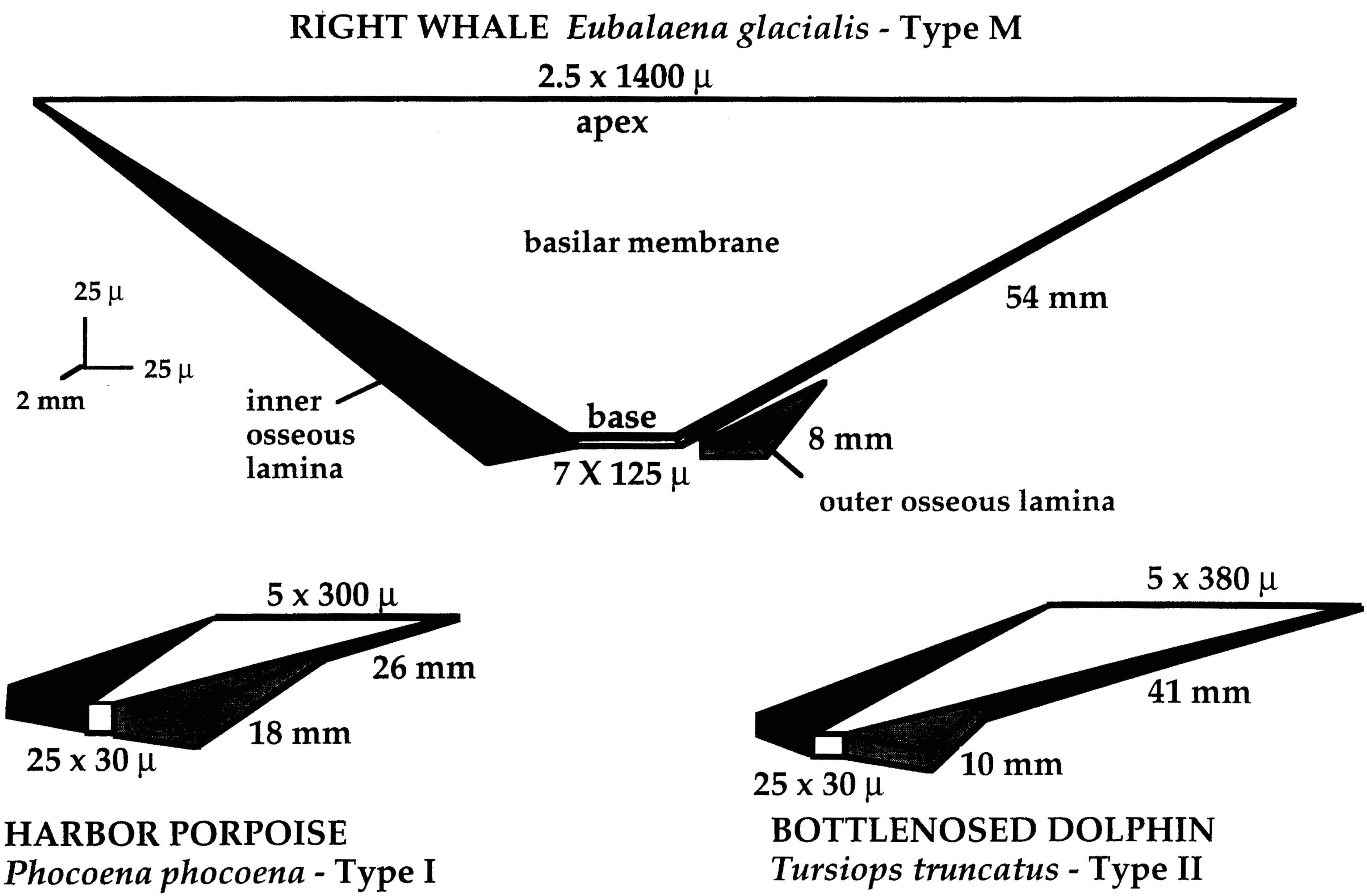


Figure 6. Differences in basilar membrane dimensions and outer laminar distributions that are primary dictates of hearing ranges in odontocetes and mysticetes are represented schematically and to scale.

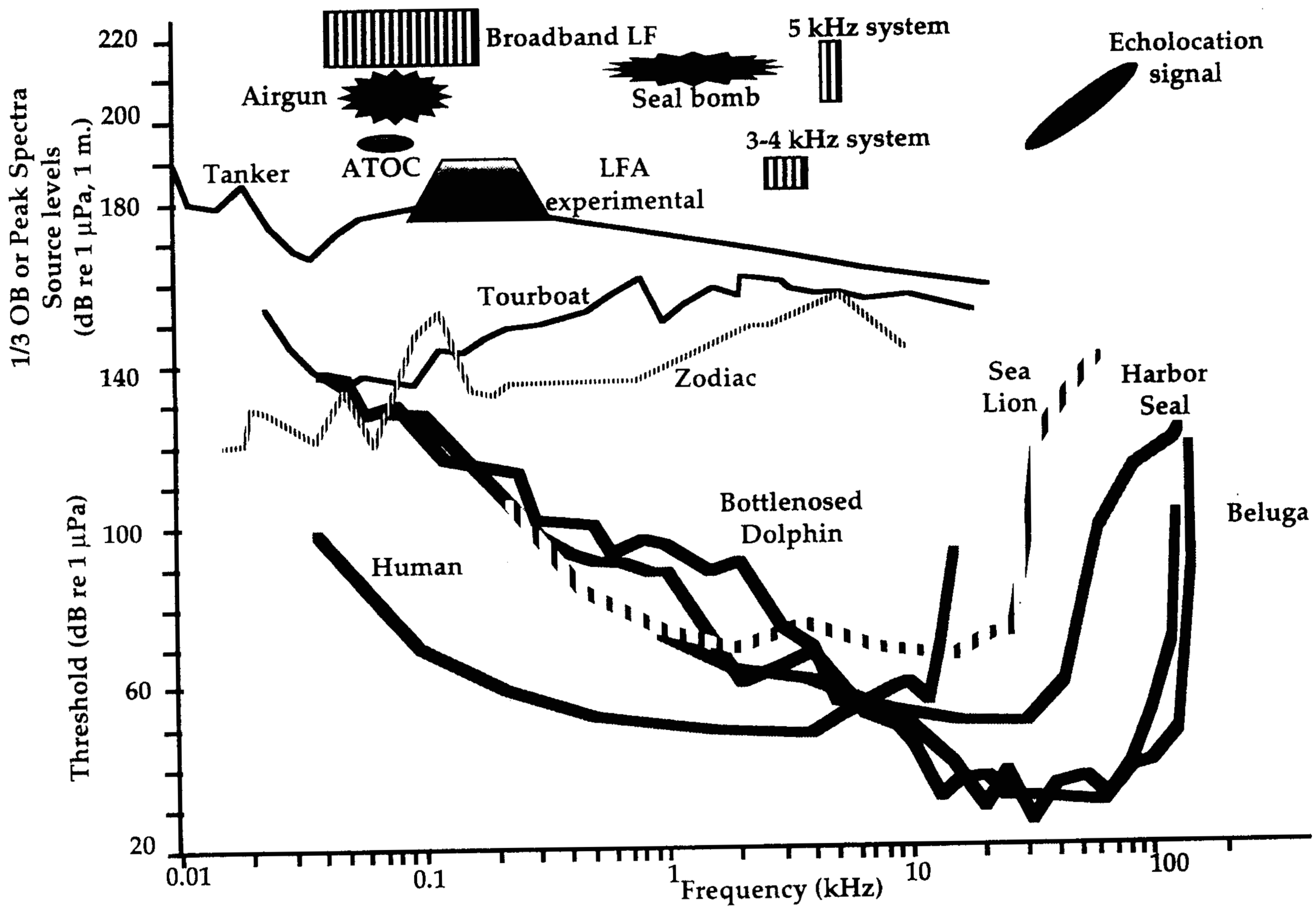


Figure 7. Audiograms for representative odontocetes and pinnipeds are compared with source level data for shipping noise (1/3 octave band) and source levels for airguns, the ATOC source, and two theoretical sonic censusing devices (Au 1995; Richardson et al 1995; Ketten, 1998). The human in-air audiogram and marine mammal underwater audiograms were recalculated as watts/$m^2$ to allow direct comparison with marine mammals before replotting on common SPL axes. If marine mammals had an equivalent relationship between sensitivity and onset of TTS as that reported for human and land mammals, any source providing a received level greater than 80 dB over the audiograms has significant potential to produce TTS. Note that the data shown are source levels at 1 m. . Bear in mind that this figure offers only gross comparisons. Because of the variable nature of the measures reported here, exact comparisons are not intended. Equally important, received levels, which are the key to estimating the probability of threshold shifts, will vary considerably depending upon the animal's proximity and the acoustic propogation characteristics of the area. (Adapted from Ketten, (1998).

# RECENT TECHNICAL MEMORANDUMS

Copies of this and other NOAA Technical Memorandums are available from the National Technical Information Service, 5285 Port Royal Road, Springfield, VA 22167. Paper copies vary in price. Microfiche copies cost $9.00. Recent issues of NOAA Technical Memorandums from the NMFS Southwest Fisheries Science Center are listed below:

NOAA-TM-NMFS-SWFSC- 246 The physical oceanography off the Central California coast during May-June, 1996: A summary of CTD data from pelagic juvenile rockfish surveys.
K.M. SAKUMA, F.B. SCHWING, K. BALTZ, D. ROBERTS, and S. RALSTON
(September 1997)

247 Killer whales of California and Western Mexico: A catalog of photo-identified individuals.
N.A. BLACK, A. SCHULMAN-JANIGER, R.L. TERNULLO, and M. GUERRERO RUIZ
(September 1997)

248 U.S. Pacific Marine Mammal Stock Assessments: 1996
J. BARLOW, K.A. FORNEY, P.S. HILL, R.L. BROWNELL, JR., J.B. CARRETTA, D.P. DeMASTER, F. JULIAN, M.S. LOWRY, T. RAGEN, and R.R. REEVES
(October 1997)

249 Analysis of agency costs attributable to the recovery plan for Sacramento River winter-run chinook salmon.
C. THOMSON
(October 1997)

250 A report of cetacean acoustic detection and dive interval studies (CADDIS) conducted in the southern Gulf of California, 1995.
J. BARLOW, K. FORNEY, A. VON SAUNDER, and J. URBAN-RAMIREZ
(December 1997)

251 Active towed-array acoustic system design study for yellowfin tuna in the eastern tropical Pacific fishery area.
C. DAVID REES
(May 1998)

252 Issues and options in designing and implementing limited access programs in marine fisheries.
S.G. POOLEY and the NMFS LIMITED ACCESS WORKING GROUP
(May 1998)

253 Recommended recovery actions for the Hawaiian monk seal population at Midway Island.
W.G. GILMARTIN and G.A. ANTONELIS
(May 1998)

254 Investigation of the potential influence of fishery-induced stress on dolphins in the eastern tropical Pacific Ocean: Research planning.
B.E. CURRY and E.F. EDWARDS
(June 1998)

255 Marine harvest refugia for west coast rockfish: a workshop.
M.M. YOKLAVICH, editor
(August 1998)