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

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National Oceanic and Atmospheric Administration
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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,

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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

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
		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, down-sweeps	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

Megaptera novaeangliae	Humpback whale	whistles[e], chirps[e]	1.5-5	1.5-2.5	-	Thompson *et al.* 1979
		clicks[e]	16-28	-	-	Thompson *et al.* 1979
		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.

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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)**.

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Dolphin-Safe Research Program Detection Technology Reports

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

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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:

$$f = c / \lambda \tag{1}$$

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° 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):

$$I = P / a = Fv / a = pv \tag{2}$$

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 (p):

$$u\,(x,t) = p / pc \tag{3}$$

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):

$$I = pv = p\,(p / pc) = p^2 / pc \tag{4}$$

The product pc 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, p=0.0013 g/cc; for sea water, p=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 ($I_{air} = I_{water}$):

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

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:

$$\begin{aligned} \text{dB SPL} &= 10 \log (p_m{}^2/p_r{}^2) \\ &= 20 \log (p_m/p_r) \end{aligned} \qquad (6)$$

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,

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

(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:

$$f = (1/2\pi) \tag{8}$$

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