

atively little difference in the overall in-air versus 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 the California sea lion, have "opted" evolutionarily for a slight edge in air.

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 versus aquatic stimuli. Minimal intensity discrimination (3 dB) by California sea lions is poorer than that of dolphins or humans (Moore and Schusterman 1976); typical frequency discrimination limens for several phocids and the sea lion (1% to 2% rdl) (Møhl 1967; Schusterman and Moore 1978a,b; Schusterman 1981) are similar to some of the bottlenose 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 to 30 kHz) were on a par with those of most odontocetes at those frequencies (18 to 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, that is, significantly poorer than those of fur seals, harbor seals, 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 CRs, 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 through the external canal, but they also found that underwater, the most sensitive region was located below the mea-

tus 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 few 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 Amazon manatee 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 the West Indian manatee 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 to 8 octaves) is narrower than that of bottlenose dolphins (10.5 octaves: 0.15 to 160 kHz; Au 1993) and phocid seals (8 to 9 octaves: 0.08 to 40 kHz; Kastak and Schusterman 1995, 1996) that have been tested over a wide range of frequencies. Best thresholds for manatees (50 to 55 dB re 1 μ Pa) are similar to in-water thresholds for several pinnipeds (45 to 55 dB re 1 μ Pa), but are significantly higher than those for odontocetes tested in similar conditions (30 to 40 dB re 1 μ Pa). 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 and 20 kHz). In terms of level and shape, therefore the West Indian manatee audiogram 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 West Indian manatee hearing, found a maximal upper frequency limit (35 kHz), which 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 the Amazon manatee between 5 and 10 kHz with thresholds of 60 to 90 dB re 1 μ Pa. Klishin et al. (1990) reported best sensitivities to underwater stimuli in the West Indian manatee 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. 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 (1956) more general description of their hearing.

Noise Trauma

One area that is relatively unexplored audiometrically is marine mammal susceptibility to hearing loss. Particularly when data are obtained from one animal, it is important to consider whether that hearing curve is representative of the normal ear for that species. Age and/or exposure to noise can significantly alter hearing in mammals. Hearing losses are recoverable (TTS, temporary threshold shift) or permanent (PTS) according to the extent of inner ear damage (for reviews, see Lipscomb 1978, Lehnhardt 1986, Richardson et al. 1991). Damage location and severity are correlated with the power spectrum of the signal in relation to the sensitivity of the animal. For narrow-band, high frequency signals, losses typically occur in or near the signal band, but intensity and duration can act synergistically to broaden the loss. Long or repeated exposures to TTS level stimuli without adequate recovery periods can induce permanent threshold shifts. In general, if the duration of intense noise is short and the noise is narrow and not impulsive, hearing is recoverable and the loss is near the signal's peak frequency. If exposure is long, or if the signal is broadband with a sudden onset, some hearing, particularly in the higher frequencies, can be permanently lost.

In humans, PTS results most often from protracted, repeat intense exposures (e.g., occupational auditory hazards from background noise) or sudden onset of intense sounds (e.g., rapid, repeated gun fire). Acoustic trauma induced by sudden onset, loud noise (a "blast" of sound) is not synonymous with blast trauma, nor are noise and blast effects of the same magnitude. Blast injuries generally result from a single exposure to an explosive shock wave that has a compressive phase with a few microseconds initial rise time to a massive pressure increase over ambient followed by a rarefactive wave in which pressure drops well below ambient. Blast damage may be repairable or permanent according to the severity of the single blast exposure. Hearing loss with aging (presbycusis), in contrast, is the accumulation of PTS and TTS insults to the ear. Typically, high frequencies are lost first with the loss gradually spreading to lower frequencies over time.

In experiments, multihour exposures to narrow band noise are used to induce PTS. Most mammals incur losses when the signal is 80 dB over the animal's threshold. Temporary threshold shift has been produced in humans for frequencies between 0.7 and 5.6 kHz (our most sensitive range) from underwater sound sources when received levels were 150 to 180 dB re 1 μ Pa (Smith and Wojtowicz 1985, Smith et

al. 1988). Taking into account differences in measurements of sound pressure in air versus water (equations 4 and 5), these underwater levels are consistent with the 80- to 90-dB exposure levels that induce TTS in humans at similar frequencies in air. Sharp rise-time signals produce broad spectrum PTS at lower intensities than slow onset signals both in air and in water (Lipscomb 1978, Lehnhardt 1986).

Currently, there are insufficient data to determine accurately TTS and PTS exposure guidelines for any marine mammal. Although there is the possibility that dive-related adaptations ameliorate acoustic trauma, recent studies show losses in marine mammals consistent with age-related hearing changes (Ketten et al. 1992, 1995). Significant differences in the hearing thresholds of two California sea lions reported by Kastak and Schusterman (1995) are consistent with age-related hearing differences between the animals. In odontocetes, postmortem examinations of ears from older bottlenose dolphins with known hearing losses found neural degeneration patterns similar to those of older humans, which are consistent with a progressive, profound high frequency loss (Ketten et al. 1995).

It is likely that all marine mammals can be impacted by sound at some combination of frequency and intensity, but those parameters will vary considerably by species. In terms of research, the possibility of a hearing loss from both natural and anthropogenic acoustic impacts should be considered in the interpretation of the data for any animal for which there is little or no history. The possibility of hearing loss over time needs to be tested with long-term studies and should be considered in interpreting data from older animals. Finally, as we expand our use of ocean technologies that have direct and indirect sonic effects, we must be aware of their potential to produce acoustic impacts in ranges important for aquatic species.

Ears

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

EXTERNAL EAR. Pinnae are absent, although vestigial pinnal rings occur in some individuals. External auditory canals are present in cetaceans, but it is debatable whether they are functional. In odontocetes, the external canal is ex-

ceptionally 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 because the transmission characteristics of blubber and seawater 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 bottlenose dolphin 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 [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 (Fig. 4-6).

Several forms of data support this hypothesis. The fats in the mandible are wax esters with acoustic impedances close to seawater (Varanasi and Malins 1971). Evoked responses

and cochlear potentials in spotted and bottlenose dolphins 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 bottlenose dolphin 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 as the lateral fatty lobes are near the meatus in delphinids. No discrete soft tissue channels to the ear have as yet been identified in mysticetes.

TYMPANOPERIOTIC COMPLEX. The temporal bones of cetaceans are distinctive in both form and construction. The inner ear is housed in the periotic, which is fused at one or more points to the tympanic, or middle ear bone. This "tympanoperiotic" bullar complex is located outside the skull in a peribullar cavity formed evolutionarily by eliminating the small, pneumatized, mastoid spaces common in terrestrial animals. The periotic and tympanic are bordered laterally and ventrally by the mandible and hyoids. The extracranial position of the tympanic and periotic is important because it increases the acoustic separation of the middle and inner ears, as discussed earlier in the section on localization and interaural distances.

Tympanic and periotic volumes are highly correlated with animal size (Ketten and Wartzok 1990). Mysticete bullae are two to three times larger than those of most odonto-

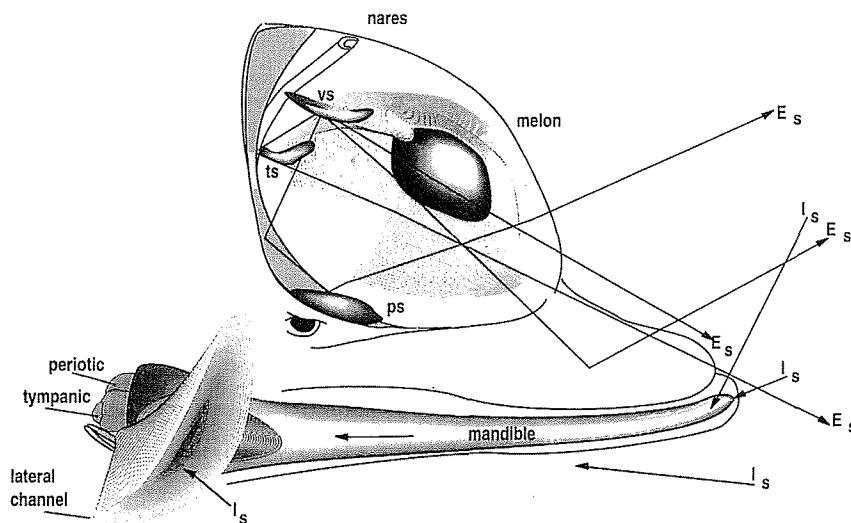


Figure 4-6. Sound paths in the dolphin head. (See also Pabst, Rommel, and McLellan, Chapter 2, this volume.) Outgoing ultrasonic signals (E_s) are generated in the vestibular (vs) and tubular (ts) nasal sac diverticulae and reflected off the cranium and premaxillary sac (ps) (Norris 1980, Au 1993). Incident sounds (I_s) from anterior targets enter the lower jaw where lipids act as preferential low-impedance acoustic conduits to the ear (Varanasi and Malins 1971, Norris 1980). Lateral, trumpetlike fatty lobes (lateral channel) with densities equal to those in the jaw overlie the pan bone and may act as additional input channels for signals from the rear or side of the animal. (Ketten 1994; figure ©Ketten 1992, revised 1997.)

cetes. Mysticete tympanics are nearly twice the volume of the periotics. In odontocetes, periotic and tympanic volumes are nearly equal. The periotic is ovoid, massive, and thick-walled in all cetaceans. The odontocete tympanic is thin-walled and conical, tapering anteriorly. Mysticete tympanics are thick-walled and spherical. This means mysticetes have larger middle ear cavities with relatively low frequency resonance characteristics compared to smaller, higher resonance odontocete middle ear cavities. The fine structure of the tympanoperiotic and the solidity of the tympanoperiotic suture differ among species, but no specific auditory effect has been determined for these differences (Kasuya 1973, Ketten 1984, Ketten and Wartzok 1990).

Odontocete tympanoperiotics 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. Because peribullar sinuses are most extensive in riverine, ultra-high frequency species; like the bottlenose, and are poorly developed in pelagic mysticetes, Oelschläger (1986) suggested that the peribullar plexus and expanded sinuses are primarily echolocation-related adaptations, functioning as acoustical isolators for the ear, and were not driven evolutionarily by diving.

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, and vary widely 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 with a conventional fibrous annular ligament. Furthermore, as noted earlier, the tympanic bone scales with animal size and is on average double the volume of the periotic. Therefore, the mysticete middle ear cavity is substantially larger than that of any odontocete and, in combination with their massive ossicles that are loosely joined, forms 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 intratym-

panic 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, pers. comm.) 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 (McCormick et al. 1970, 1980; Lipatov and Solntseva 1972; Fleischer 1978). On the basis of experiments with anesthetized bottlenose dolphin 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 tympanoperiotic joints; Fleischer's requires a mobile stapes, distensible round window, and flexible tympanoperiotic 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, and Fleischer's data were subject to postmortem 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.

In all cetaceans, the vestibular system is substantially smaller in volume than the cochlea and may be vestigial (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 re-

Table 4-2. Auditory, Vestibular, and Optic Nerve Distributions

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

Data compiled from Yamada 1953; Gacek and Rasmussen 1961; Jansen and Jansen 1969; Firbas 1972; Morgane and Jacobs 1972; Bruns and Schmieszek 1980; Dawson 1980; Ketten 1984, 1992; Vater 1988a,b; Nadol 1988; Gao and Zhou 1991, 1992, 1995; Kössl and Vater 1995.

^aDensities at auditory fovea as described by Bruns and Schmieszek (1980).

duced as well (Table 4-2); on average less than 5% of the cetacean VIIIth nerve is devoted to vestibular fibers (Fig. 4-4), 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 cetaceans 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).

All cetacean cochleae have three scalae or chambers like other mammals (Figs. 4-4 and 4-7): 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). We briefly summarize histological observations and discuss in detail only the cochlear features that 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,b,c, 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, Ketten and Wartzok 1990, Solntseva 1990). Most of the hypercellularity is associated with the support cells of the basilar membrane and with the stria vascu-

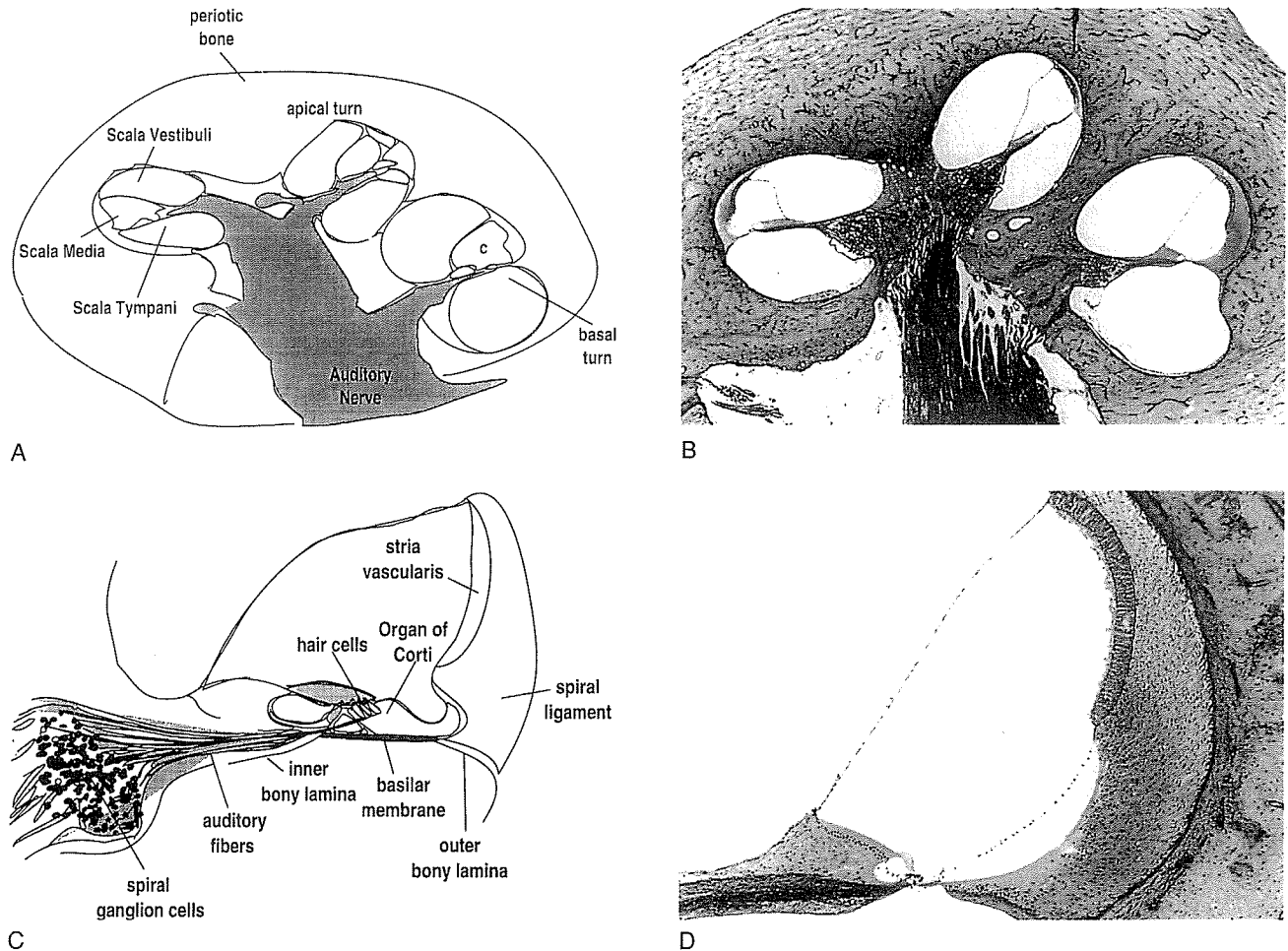


Figure 4-7. (A) A schematic of a typical dolphin cochlea is shown in cross-section with a corresponding photomicrograph (B) from a 25- μm histologic section of a *Phocoena* ear. (C) A schematic of the major features of the cochlear duct in the high-frequency basal region that are equivalent to the magnified view (D) of a 25- μm section of an Atlantic white-sided dolphin inner ear.

laris, 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 postmortem times before they are preserved.

The fiber and ganglion cell counts for the auditory nerve are exceptional in all cetaceans (Table 4-2). 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 threefold greater than in other mammals. Comparisons of the ratios of auditory, vestibular, and optic nerve fibers in cetaceans versus representative land mammals (Table 4-2) underscore the hypertrophy of the cetacean auditory nerve. The vestibular to auditory ratios are approximately 1/10 those of land mammals. Optic to auditory ratios in Type II odontocetes and mysticetes are approximately half those of most land mam-

mals (noting an exception for the exceptionally high human optic value), whereas those of Type I riverine odontocetes are an order of magnitude less.

Auditory ganglion cell densities in Type I odontocetes are particularly notable, averaging more than 3000 cells/mm. Using a mammalian average of 100 inner hair cells/mm (Kiang, pers. comm.) and four rows of outer hair cells/inner hair cell, these 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 (*Felis domesticus*), 3:1; and in bats, the average is 4:1 (Firbas 1972, Bruns and Schmieszek 1980, Vater 1988b). Because 90% to 95% of all afferent spiral ganglion cells innervate inner hair cells, the average ganglion cell to inner hair cell ratio is 24:1 for cetaceans, or more than twice the average ratio in bats and three times that of humans. Wever et al. (1971c) speculated that additional innervation is required primarily in the basal region to relay greater detail about ultrasonic signals to the central nervous system in echolocation analyses.

Electrophysiological results are consistent with this speculation. The central nervous system 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, that is, 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, although 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 sim-

ilarity of odontocete and mysticete innervations suggests that mysticetes may have equally complex processing but possibly for infra- rather than ultrasonic tasks.

CETACEAN INNER EAR STRUCTURE—HEARING CORRELATES. The cetacean basilar membrane is a highly differentiated structure with substantial variations in length, thickness (T), and width (W) (Table 4-3, Fig. 4-8). 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 to 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). In odontocetes thicknesses

Table 4-3. Cochlear Morphometry in Whales versus Land Mammals

Species	Common Name	Cochlear Type	Turns	Membrane Length (mm)	Outer Lamina (mm)	Base Thickness (μm)	Base Width (μm)	Apex Thickness (μm)	Apex Width (μm)	Basal T:W Ratio	Apical T:W Ratio
<i>Imia geoffrensis</i>	Boutu	I	1.5	38.2	^a						
<i>Phocoena phocoena</i>	Harbor porpoise	I	1.5	22.5	17.6	25	30	5	290	0.83	0.017
<i>Grampus griseus</i>	Risso's dolphin	II	2.5	41.0	^a	20	40	5	420	0.50	0.012
<i>Lagenorhynchus albirostris</i>	White-beaked dolphin	II	2.5	34.8	8.5	20	40	5	360	0.50	0.014
<i>Stenella attenuata</i>	Spotted dolphin	II	2.5	36.9	8.4	20	40	5	400	0.50	0.013
<i>Tursiops truncatus</i>	Bottlenosed dolphin	II	2.25	38.9	10.3	25	35	5	380	0.71	0.013
<i>Physeter catodon</i>	Sperm whale		1.75	54.3	^a						
<i>Balaenoptera acutorostrata</i>	Minke	M	2.25	50.6		—	100	—	1500		
<i>Balaena mysticetus</i>	Bowhead	M	2.25	56.5	< 10 ^b	7.5	120	2.5	1670	0.06	0.001
<i>Balaenoptera physalus</i>	Fin whale	M	2.5	64.7		—	100	—	2200		
<i>Eubalaena glacialis</i>	Right whale	M	2.5	54.1	< 8 ^b	7	125	2.5	1400	0.06	0.002
<i>Rhinolophus ferrumequinum</i>	Horseshoe bat	Æ	2.25	16.1	^a	35	80	2	150	0.44	0.013
<i>Pteronotus parnellii</i>	Mustached bat	Æ	2.75	14.0	^a	22	50	2	110	0.44	0.018
<i>Spalax ehrenbergi</i>	Mole rat	Sb	3.5	13.7		—	120	—	200		
<i>Cavia porcellus</i>	Guinea pig	T	4.25	18.5		7.4	70	2	250	0.11	0.008
<i>Felis domesticus</i>	Cat	T	3	28.0	^a	12	80	5	370	0.15	0.014
<i>Homo sapiens</i>	Human	T	2.5	33.0		—	120	—	550		

Data compiled from Wever et al. 1971a, b; Firbas 1972; Bruns and Schmieszek 1980; Norris and Leatherwood 1981; Ketten 1984, 1992, 1994; West 1985; Vater 1988a,b; Nadol 1988; Echterler et al. 1994; Kössl and Vater 1995.

^aOuter osseous lamina length unknown.

^bLaminar remnant present but not in contact with basilar membrane.

Width (W) = pars arcuata and pectinata; Thickness (T) = pars pectinata maximum.

I = aquatic > 100 kHz; II = aquatic < 90 kHz; M = aquatic < 2 kHz; Æ = æolian > 20 kHz; Sb = subterranean; T = terrestrial.

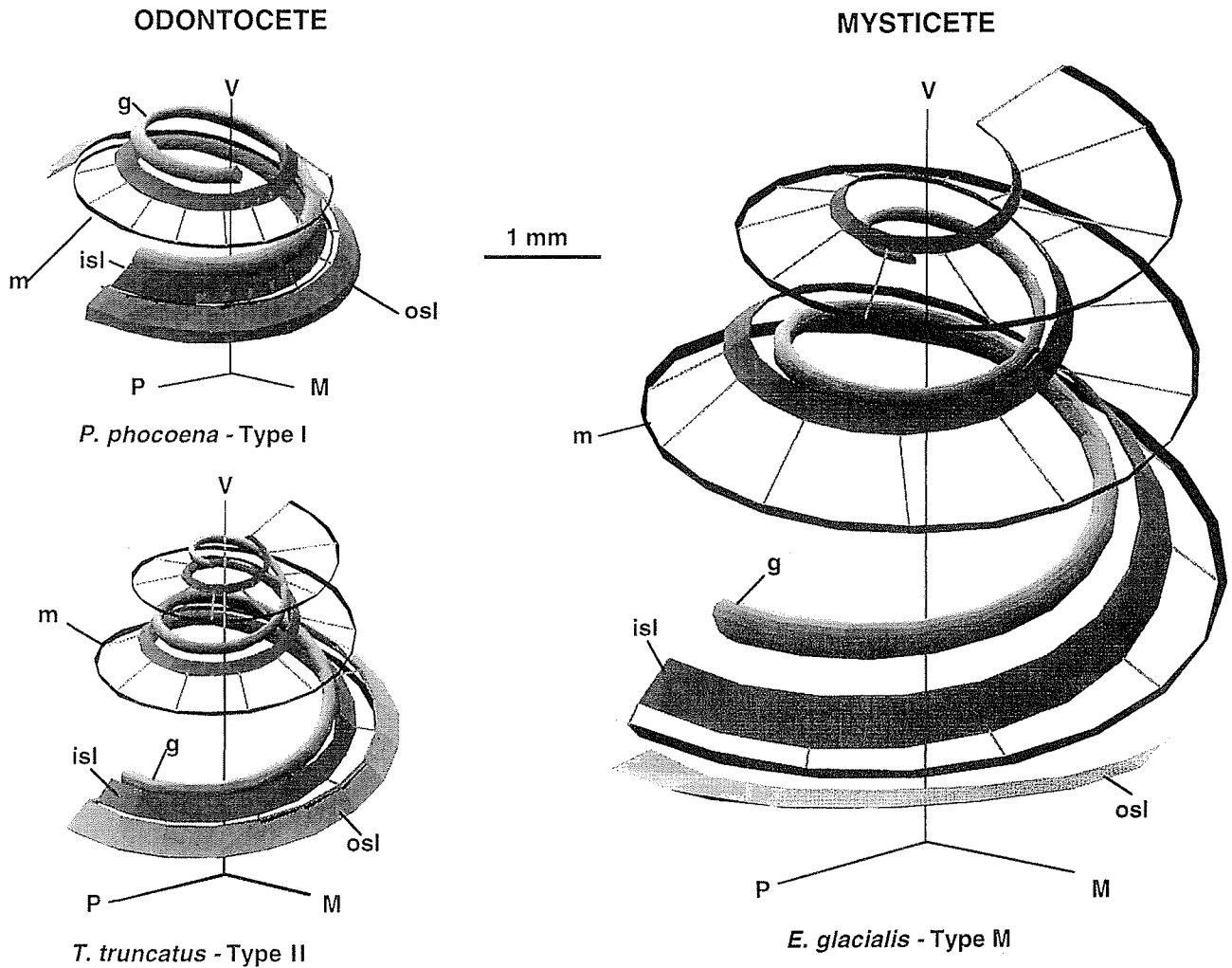


Figure 4-8. Three-dimensional schematics summarize basilar membrane dimensions and support element differences among Type I, Type II odontocete, and Type M mysticete inner ears in cetaceans. The cochlea are inverted from in vivo orientations. The schematics are drawn to the same scale for the three species illustrated (see Table 4-3). (g) spiral ganglion; (isl) inner bony spiral lamina; (m) basilar membrane; (osl) outer bony spiral lamina; (P) posterior; M (medial); (V) ventral.

typically range from $25\ \mu\text{m}$ at the base to $5\ \mu\text{m}$ at the apex (Table 4-3). Therefore, a typical cross-section of an odontocete basilar membrane is square at the base becoming rectangular apically. Mysticete membranes are thin rectangles throughout, varying in thickness between $7\ \mu\text{m}$ at the base to $2\ \mu\text{m}$ at the apex. Width gradients in mysticetes can be as great as in odontocetes with membranes in some species ranging from $100\ \mu\text{m}$ at the base (similar to the base in humans) to $1600\ \mu\text{m}$ at the apex. The apical widths in mysticetes are three times that of human, three to five times those of most odontocetes, and 1.2 times that of elephants, which are known to perceive infrasonics (Payne et al. 1986).

Comparing bat, odontocete, and mysticete basilar membrane thickness to width (T:W) ratios is a good exercise in structure-function relationships. T:W ratios are consistent with the maximal high and low frequencies each species

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

A striking feature of odontocete basilar membranes is their association with extensive outer bony laminae. In mammals, ossified outer spiral laminae are hallmarks of ultrasonic ears (Yamada 1953, Reysenbach de Haan 1956, Sales and Pye 1974, Ketten 1984). Thick outer bony laminae (Fig. 4-7C) are present throughout the basal turn in all odontocetes, and the proportional extent of outer laminae is functionally correlated with odontocete ultrasonic frequency ranges (Ketten and Wartzok 1990). In the basal, high frequency region of the cochlea, odontocete basilar membranes resemble thick girders, stiffened by attachments at both margins to a rigid bony shelf. In Type I echolocators with peak frequencies above 100 kHz an outer lamina is present for 60% of the cochlear duct (Fig. 4-8). Type II echolocators with lower peak frequencies have a bony anchor for about 30% of the duct. Therefore, the Type I basilar membrane is coupled tightly to a stiff ledge for twice as much of its length as a Type II membrane. If Type I and II membranes have similar thickness:width ratios, a Type I cochlea with longer outer laminae would have greater membrane stiffness and higher resonant frequencies than an equivalent position in a Type II membrane without bony support. Both membrane ratios and the extent or proportion of auxiliary bony membrane support are important mechanistic keys to how odontocetes achieve ultrasonic hearing despite ear size.

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

Pinnipeds

EXTERNAL EAR. Pinniped ears are less derived than cetacean ears. The external pinnae are reduced or absent. Ear canal diameter and closure mechanisms vary widely in pinnipeds, and the exact role of the canal in submerged hearing has not clearly been determined. Otariids have essentially terrestrial, broad-bore external canals with moderate to distinctive pinnae. Phocids, particularly northern elephant seals, spend more time in water than otariids and have only a vestigial cartilaginous meatal ring, no pinnae, and nar-

row ear canals (D. R. Ketten and R. J. Schusterman, unpubl.). Although the phocids have no external pinnae, it is not yet known which species normally have air-filled versus partially to fully blocked external canals. No specialized soft tissue sound paths for underwater hearing have been clearly demonstrated in seals.

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

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

MIDDLE EAR. Pinniped middle ears have a moderate layer of cavernous tissue, but it is less developed than that of cetaceans (Møhl 1968, Ramprashad et al. 1972, Repenning 1972, Fleischer 1978). Pinniped ossicular chains are diverse. Those in otariids resemble terrestrial carnivores; ossicles of

phocids are more massive but with wide species variation in shape (Doran 1879, Fleischer 1978), which suggests a wider range of peak frequencies and more emphasis on lower frequency reception than in otariids. Although some researchers indicate phocids have small eardrums (Repenning 1972), the size is not significantly different from that of equivalent mass land mammals. The oval and round window areas in terrestrial mammals are of approximately the same size. In pinnipeds, the oval window can be one-half to one-third the size of the round window. Eardrum to oval window ratios have been cited frequently as a factor in middle ear gain, but this association is still being debated (Rosowski 1994), and depending on the exact size distributions among these three membranes in each pinniped species, there could be wide differences in middle ear amplification among pinnipeds.

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

Sirenians

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

EXTERNAL EAR. Exact sound reception paths are not known in sirenians. The unusual anatomy of the zygomatic arch in manatees, combined with its relation to the squamosal and periotic have made the zygomatic a frequent candidate for a sirenian analogue to the odontocete fat channels. The periotic is tied by a syndesmotic (mixed fibrous tissue and bone) joint to the squamosal, which is fused, in turn,

to the zygomatic process, a highly convoluted cartilaginous labyrinth filled with lipids. The zygomatic is, in effect, an inflated, oil-filled, bony sponge that has substantial mass but less stiffness than an equivalent process of compact bone (Domning and Hayek 1986, Ketten et al. 1992). In the Amazonian manatee, the best thresholds in evoked potential recordings were obtained from probes overlying this region (Bullock et al. 1980, Klishin et al. 1990), but no clear acoustic function has been demonstrated.

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

INNER EAR. The sirenian inner ear is a mixture of aquatic and land mammal features. Anatomically, *T. manatus* inner ears are relatively unspecialized. The cochlea has none of the obvious features related to ultra- or infrasonic hearing found in cetacean ears. Basilar membrane structure and neural distributions are closer to those of pinnipeds or some land mammals than to those of cetaceans (Ketten et al. 1992). The outer osseous spiral lamina is small or absent, and the basilar membrane has a small base-to-apex gradient. At the thickest basal point, the membrane is approximately 150 μm wide and 7 μm thick; apically it is 600 μm by 5 μm . Therefore, the manatee has a relatively small basilar membrane gradient compared to cetaceans, which is consistent with the audio-

metric profile and 7-octave hearing range recently reported for the West Indian manatee (Gerstein et al. 1993). Spiral ganglion cell densities (500/mm) are low compared to those of odontocetes, but auditory ganglion cell sizes (20 $\mu\text{m} \times 10 \mu\text{m}$) are larger than those of many land mammals.

The intracranial position of the periotic has important implications for sound localization abilities in manatees. Depending on the sound channels used, the manatee IATD could range from a minimum of 58 μsec (intercochlear distances) to a maximum of 258 μsec (external intermeatal path). If manatees fit the conventional mammalian IATD frequency regression, the potential IATDs imply that the West Indian manatee should have an upper frequency limit of at least 50 kHz, similar to that of a smaller odontocete. To date, there is no indication that any species of manatee has acute ultrasonic hearing (Schevill and Watkins 1965; Bullock et al. 1980, 1982; Klishin et al. 1990; Popov and Supin 1990a). Intensity differences from head shadow could provide some directional cues, but the available anatomical data (Ketten et al. 1992) suggest that manatees may have difficulty using phase cues for sound localization and have poorer localization ability than other marine mammals.

Localization ability is of particular interest in Florida manatees because of the number injured annually from collisions with boats in shallow coastal waters and canals. Since manatee salvage programs began throughout Florida in 1971, more than 2400 dead manatees have been recovered (D. Odell, pers. comm.). Human activities may account, directly or indirectly, for one-third to one-half of all deaths during the past 15 years. Even more important, deaths from collisions doubled in the past decade. In 1991, more than 30% of all deaths were associated with boats (Ketten et al. 1992). Although the sound spectra for most outboard motors are well within what we believe to be the hearing range of Florida manatees, the ability to determine a boat's direction depends on the ability to localize engine noise. Therefore, the collision hazard could be related more to localization abilities than to hearing range or sensitivity per se.

Is the conclusion that sirenians have less localization ability than cetaceans tenable? Did environmental pressures that influenced the evolution of sirenians differ in some important way from those of their terrestrial counterparts and from other marine mammals that are consistent with proposed differences in hearing? The tympanoperiotic complexes of extinct Sirenians are remarkably similar to those of modern West Indian manatee. The structural commonalities between fossil and modern manatee ears imply that few functional changes have occurred in the sirenian auditory periphery since the Eocene. Sirenians first appear in the fossil record in the early Eocene and were already adapted to at least a partially aquatic lifestyle by the early to middle

Eocene (Barnes et al. 1985). Their closest affinities are with proboscideans and tethytheres, and, like cetaceans, they arose from unknown ungulate stock. A radiation in the late Eocene led to modern dugongids and trichechids. The West Indian manatee is a docile, slow grazer that lives in fresh or estuarine environments. The Florida manatee averages 400 kg and 3 m, but can exceed 4 m in length (Ridgway 1972, Odell et al. 1981). They cruise at an average speed of 3 km/hr and seldom attain speeds more than 20 km/hr even when alarmed (Reynolds 1981). For most mammals, sounds related to predators, mates, and food sources are important selection pressures. With the exception of Steller's sea cow (*Hydrodamalis gigas*), sirenians have been tropical animals, feeding on marine angiosperms or sea grasses, since the Eocene (Domning 1977, 1981; Eva 1980; Domning et al. 1982). Trichechids therefore developed in a relatively stable environment with few predators, and it is unlikely they use sound to detect food. If acoustic cues carried little or no survival advantage, acoustic developments in ancestral species may have been lost. The limited data on manatees are intriguing because of the diversity of the results. Relatively little is known about masking or localization in any sirenian, and we have no direct data for the dugong. Given their size and salt water habitat, it is likely that dugongs evolved somewhat different sensory abilities from trichechids.

If hearing is not highly evolved in manatees, are there other candidates for a premier sensory system? A highly developed chemosensory apparatus would be useful for a shallow water herbivore, and the dimensions of chorda tympani hint that gustation could be an important sense in sirenians. On the other hand, peripheral targets for chorda tympani in manatees have not been determined, and innervation patterns in marine mammals do not always match those of terrestrial species. Exceptional vibrissal discrimination has been demonstrated for pinnipeds (Dehnhardt 1990, 1994; Kastelein 1991) and suggests similar investigations with sirenians would be worthwhile.

Fissipeds and Ursids

These groups are linked by a lack of data. Remarkably little is known about sea otter hearing even in comparison to the sirenians, and data on polar bear hearing or ear adaptations appear to be nonexistent.

The sea otter has a well-defined external ear flap and a canal that is open at the surface. Kenyon (1981) indicated that the pinnal flange folds downward on dives, which suggests that the canal is at least passively closed during dives, but there are no data on whether specialized valves are associated with the ear canal like those found in pinnipeds. Otter auditory bullae are attached to the skull and resemble those of pinnipeds. CT scans of sea otters (D. R. Ketten, unpubl.)

show that their middle and inner ears are grossly configured like ears of similarly sized terrestrial carnivores, with the same orientation and 2.5 turn distribution. Spector (1956) and Gunn (1988) both indicated an upper frequency limit of 35 kHz for common river otters, which have similar ear anatomy.

It is reasonable to assume that in-air hearing is well-developed in polar bears but there are no published audiograms for air or underwater hearing. Considering their size, polar bears should have moderately good low frequency hearing, but because they are also aquatic, they may have evolved high frequency ear adaptations in parallel with other marine mammals. Anatomically, polar bear ears are interesting because even casual observations show that polar bears have a well-developed, moderately stiff pinnal flange resembling those of other ursids; however, because they dive in cold waters, it is likely polar bears have special mechanisms for preserving the integrity of the ear canal and middle ear. Hearing in this group clearly warrants further research, particularly because they represent an unknown level of auditory adaptation for underwater hearing.

Vision

The characteristics of marine mammal vision can be divided into two major functional categories: visual detection and visual acuity. The first relates to adaptations that maximize the opportunity for marine mammals to detect either predators

or prey in an environment that filters and attenuates light very differently than does air. After detection of an object, an animal needs to form a sufficiently clear image of the object to determine what action to take: ignore, flee, capture, etc. Because there are fewer studies of vision than of audition in marine mammals, and because many of the known adaptations are similar, cetaceans and pinnipeds will be considered together in the following discussion. We begin with a consideration of light in water.

Light in the Ocean

As light passes through the water column, it is absorbed, refracted, and scattered. These effects are different depending on the wavelength of the light, the concentration of chlorophyll in the water, and the concentration and type of dissolved organic matter. Based on the differences in transmission of light in different waters, Jerlov (1976) proposed a classification scheme (Fig. 4-9) that shows the wavelength dependence for the transmission of light in different types of oceanic waters. In more coastal waters, light of longer wavelength is transmitted better, whereas in the open ocean, shorter wavelength blue light is transmitted best.

In general, the photon flux density, or downward irradiance, of the light falls off as an exponential function of the depth,

$$I_d = I_s e^{-kd}, \quad (\text{equation 8})$$

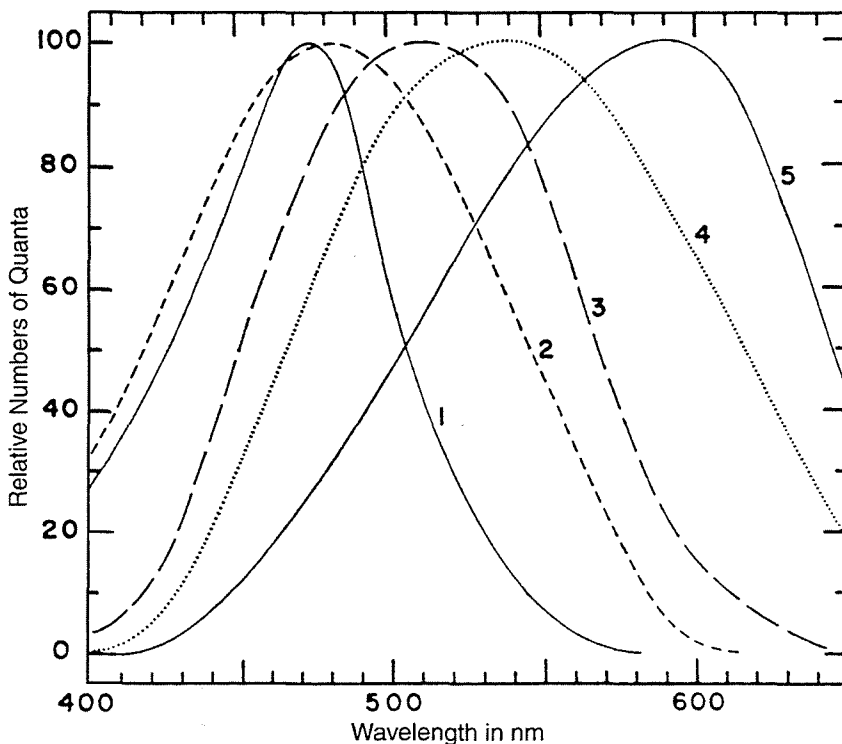


Figure 4-9. Relative spectral distribution of sunlight remaining in different marine waters, after the number of quanta at the respective maxima is reduced to 20% to 25% of the maximum number incident at the surface (wavelength = 600 nm). Curves rescaled to 100 for comparison. Curve 1 represents the spectral distribution of quanta in the clearest oceanic water at 70 m depth; curve 2, average oceanic water at 22 m; curve 3, clearest coastal water at 12 m; curve 4, average coastal water at 5 m; and curve 5, average inshore water at 3 m. (Reprinted from Munz 1965 ©Little Brown and Company.)

where I_d is the downward irradiance at depth d , I_s is the irradiance at the surface, and k is the attenuation coefficient. Light of a wavelength around 475 nm penetrates the best through clear oceanic waters (Fig. 4-9, curve 1). For light of this wavelength in typical oceanic waters (Jerlov type IB, Jerlov 1976), k is approximately 0.033 and the irradiance falls by 90% for approximately every 70 m of depth. In bright daylight, the surface irradiance for photons of 475 nm wavelength is about 1.6×10^{14} /cm²/sec or 0.67 W/m² (McFarland and Munz 1975).

Visual Detection

With the rapid attenuation of light with depth, how deep can marine mammals use vision to detect predators or prey? Lavigne and Ronald (1972) found that the minimum light level needed for a dark-adapted harp seal to distinguish between light and dark was 1.35×10^{-9} W/m² at light of a wavelength of 475 nm. The bright day surface irradiance decreases to 10^{-9} W/m² at approximately 615 m. Hence, this is the likely depth limit for visual detection in this species. Wartzok (1979) reported a somewhat greater depth value for spotted seals (*Phoca largha*) (670 m). The irradiance of the night sky with a full moon is about six orders of magnitude less than that of bright sunlight. Hence, on a bright moonlight night, irradiance decreases to 10^{-9} W/m² at about 200 m. Thus, the seal that could detect light at 615 m during the day would have to move about 415 m closer to the surface to do equally well on a moonlit night. We do not know the minimum light level actually required to detect prey because the experiments only measured the limits of light detectability. Light levels for prey detection are likely somewhat greater than these minimum levels. Assuming they are 100 times greater, or 10^{-7} W/m²,

the comparative depths for prey detection under sunlight and moonlight become 476 and 61 m, respectively. The difference in depths remains 415 m because the ratio of intensities in equation 6 at functional depth in sunlight and functional depth in moonlight remains constant.

So far we have been considering only the downwelling light, that is, light that would be sensed by a detector looking straight up. For predator or prey detection, the light coming at other angles is equally important. Figure 4-10 shows the relative intensity of light at other angles. Regardless of water type, the light scattered back toward the surface is only about 1/100 that of the light downwelling. This gives an indication of the significant advantage a predator has when approaching another animal from below. A predator looking up sees the prey as a shadow blocking light that is about two orders of magnitude more intense than the light against which the prey can detect a predator below. Typical countershading of animals minimizes this difference in light intensity. A dark dorsal surface helps the animal reflect no more light toward the surface than upwells naturally from the open ocean at that depth. A pale ventral surface helps camouflage an animal against the brighter light downwelling from above, although the difference in downwelling and upwelling light is so great that an animal which is not bioluminescent cannot match the intensity of the downwelling light and will always appear as a darker object against a lighter background. Many marine predators, such as seals and sea lions (Hobson 1966), typically attack prey from below for this reason.

To maximize the detection of prey at depth, a predator attacking from below should adopt several sensory strategies, including matching receptor pigment sensitivity to downwelling light, increasing density of photoreceptors, and enhancing photon capture by an elaborated tapetum. All of

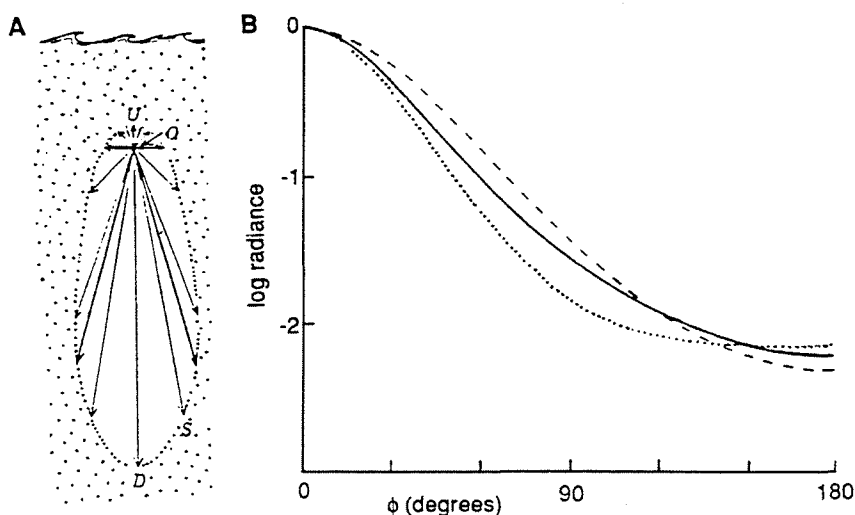


Figure 4-10. (A) Diagram of distribution of radiance found in the sea. For a given point, O, the distribution in three dimensions is given by the surface formed by revolving the dotted line S around the axis UD. The relative radiance in a given direction is the length of the line in that direction joining the point O to a point on the surface S. (B) The log radiance of light is plotted against ϕ , the angle between a given direction and the downward vertical axis. The log radiance for $\phi = 0$ has been made equal to zero. (Solid line) Lake Pend Oreille (after Tyler 1960); (dashed line) from an equation given by Tyler (see Denton et al. 1985); (dotted line) for oceanic Mediterranean waters (after Lundgren 1976, cited by Jerlov 1976). (Reprinted from Denton 1990 ©Cambridge University Press.)

these strategies will be discussed. The photoreceptors should have their greatest visual sensitivity at the same wavelength as the light that is best transmitted through the type of ocean waters in which they typically feed (Munz 1965). For both pinnipeds (Lavigne and Ronald 1975b) and cetaceans (McFarland 1971), pigments in the rod receptors (the retinal receptors specializing in low light level sensitivity) of species that feed in the open ocean have a maximum sensitivity at the blue end of the spectrum, matching the wavelengths of light that best penetrate in the open ocean.

Detection of a visual signal depends on the number of photons captured. Marine mammals maximize their visual sensitivity by having a high density of photoreceptors and a well-developed tapetum. The California sea lion has receptor densities of 200,000 to 260,000 per mm² (Landau and Dawson 1970) and the bottlenose dolphin has 400,000 per mm² (Dral 1977), compared to 120,000 to 160,000 in humans (Østerberg 1935) and 800,000 in a nocturnal fish, the lota (Walls 1942).

The tapetum, a reflective layer behind the retina, reflects the photons that were not absorbed by the visual pigment as the light initially passed through the visual receptor layer. This reflection gives the visual pigment a second chance to capture a photon and thus increases the probability of detection. Marine mammals have the most developed tapeta of any mammal (Walls 1942, Dawson 1980). The tapeta are thicker, up to 35 layers in the gray seal (*Halichoerus grypus*) (Braekevelt 1986), and back the entire fundus (Nagy and Ronald 1970, Dawson et al. 1972, Braekevelt 1986). Even at the periphery of the tapetum, the average number of cell layers, 15 to 20, is as many as at the center of the tapetum in terrestrial nocturnal predators such as the cat (Pedler 1963). Dawson et al. (1987a) noted that the tapetum of a Risso's dolphin (*Grampus griseus*) (a pelagic species) reflected more blue light than that of a bottlenose dolphin (a coastal species). This difference is consistent with the sensitivity hypothesis for detection, but Dawson et al. (1987a) cautioned against building too much of a case on the basis of one Risso's dolphin specimen. All 11 bottlenose dolphins observed were very similar to each other in spectral light reflected by the tapetum.

In shallower depths, down to approximately 100 m in the open ocean, the downwelling light still has a relatively broad range of wavelengths. In this depth range, a predator can use a second method to detect prey, the contrast method (Lythgoe 1968). For contrast detection, the pigment in the eye needs to have its best sensitivity offset somewhat from the wavelength that best penetrates the ocean. To understand why we need to remember that the wavelength-dependent absorption as light passes through oceanic water will be the same for all light paths. This means that in the first 100 m of

the ocean, downwelling light has a range of wavelengths consistent with a 100-m path but an animal looking horizontally would see light that had passed through thousands of meters of ocean, and thus would see light restricted to the narrow band of wavelengths that are best transmitted. A silver-sided fish that reflected the horizontal light perfectly would be invisible to a predator looking horizontally. However, if the fish also reflected some of the downwelling light, it would be reflecting light of a different spectrum containing longer wavelengths than the horizontal light a predator would see on all sides of the fish. If the predator had a visual pigment with greater sensitivity to longer wavelengths of light, then the difference in the light spectrum reflected from the fish and the general horizontal background light would be detected easily. There are several lines of evidence (discussed below) that show some marine mammals have more than one type of photopigment, and thus can make use of both sensitivity (when attacking prey from below) and contrast (when attacking prey from the side).

The vertebrate photoreceptors that function best at low light levels are the rod photoreceptors. Rod pigments are most accurately measured when they are extracted from a dark-adapted eye preserved immediately after the death of the animal. Such ideal conditions cannot be met for most marine mammals, so the values for extracted pigments are less accurate than for most terrestrial mammals. In addition, many of the measurements are based on only a single specimen. Given these caveats, the current data show a basic correlation between what we know about the diving habits of some cetacean species and the peak sensitivity of the photopigment in their rods. The deep-diving Baird's beaked whale (*Berardius bairdii*) has a pigment maximum at 481 nm, whereas the gray whale (*Eschrichtius robustus*) (a coastal species) has a pigment maximum at 497 nm (McFarland 1971). Recall that shorter wavelengths are transmitted best and reach greater depths. The humpback whale (*Megaptera novaeangliae*), with a typical diving depth intermediate between the beaked whale and the gray whale, has a pigment maximum at 492 nm (Dartnell 1962). The Weddell seal (*Lep- tonychotes weddelli*) has a pigment maximum at 495 to 496 nm, similar to coastal fishes and terrestrial mammals, but the deep diving southern elephant seal (*Mirounga leonina*) (Slip et al. 1994) has a pigment maximum at 485 to 486 nm (Lythgoe and Dartnell 1970). The elephant seal pigment maximum could be the result of a shift either to the wavelengths best penetrating the depths, or to wavelengths emitted by bioluminescent prey (Young and Mencher 1980). Absorption curves from these whales and seals suggest that there is only one pigment. However, most of these studies are old and did not use sensitive tests presently available. The nocturnal New World owl monkey (*Aotus trivirgatus*) and nocturnal

prosimian bush-baby (*Galago garnetti*) used to be considered species with all rod retinas (Walls 1942), but modern monoclonal antibody techniques have identified cones in the retinas of both species (Wikler and Rakic 1990).

A variety of anatomical and behavioral evidence suggests that odontocetes, phocids, otariids, and sirenians have more than one photopigment. Anatomically, both rods and cones have been described in the retinas of bottlenose dolphins (Perez et al. 1972, Dawson and Perez 1973), Dall's porpoise (*Phocoenoides dalli*) (Murayama et al. 1992), harbor porpoise (Kastelein et al. 1990), sperm whales (*Physeter macrocephalus*) (Mann 1946), fin whales (Mann 1946), minke whales (*Balaenoptera acutorostrata*) (Murayama et al. 1992), harbor seals (Jamieson and Fisher 1971), harp seals (Nagy and Ronald 1975), and West Indian manatees (Cohen et al. 1982). Behavioral studies of critical flicker fusion frequency (the fastest flicker rates that can be detected as a flicker rather than as continuous light), indicate that the faster responding cone systems exist in harp seals (Bernholtz and Mathews 1975) and bottlenose dolphins (van Esch and de Wolf 1979). Lavigne and Ronald's (1975a) reanalysis of visual acuity studies in California sea lions conducted by Schusterman and Balliet (1971) and Schusterman (1972) indicate the presence of both rod and cone visual systems. Finally, the demonstration of color discrimination in spotted seals (Wartzok and McCormick 1978) also indicates the presence of more than one visual pigment. The difficulty with which color discrimination was demonstrated in spotted seals (Wartzok and McCormick 1978) and the inability to demonstrate it in bottlenose dolphins (Simons and Huigen 1977, Madsen and Herman 1980) suggest that these marine mammals are using their dual pigment systems primarily for brightness detection and discrimination and did not evolve them mainly for color vision.

Multiple pigment visual systems in marine mammals probably serve three functions: (1) to maximize sensitivity when at depth and approaching prey from below; (2) to maximize contrast when at shallower depths and approaching prey from the side; and (3) to allow vision in up to nine orders of magnitude of changes in light intensity. A rod system sensitive to the lowest levels of light at depth would be bleached out by the much higher intensities at or near the surface. The combination of a rod system for vision at depth and a cone system for vision near the surface, and on land in the case of pinnipeds, allows marine mammals to function visually at almost all light levels and depths. One open question is what adaptations have been made in the rod pigment to allow it to regenerate quickly enough to reach maximum sensitivity as the marine mammal dives to depth. Diving marine mammals often descend at rates of greater than 1 m/sec (Kooymann and Gentry 1986, Martin et al. 1993, Watkins et al. 1993,

Asaga et al. 1994), which translates into decreases in light intensity of about one order of magnitude, or one log unit, per min. Initial dark adaptation has only been measured in humans (Hecht and Hsia 1945) where it occurs at a rate of about 0.5 log/min. Clearly the biochemical processes of rod pigment regeneration need to be modified in marine mammals if they are to use the full potential sensitivity of their visual system. Levenson and Schusterman (1998) presented preliminary evidence that northern elephant seals dark adapt completely in 10 minutes. Given their sensitivity range, this suggests that they are adapting at a rate approaching 1 log/min, and thus operating with near maximum sensitivity at most depths.

There is good evidence that freely diving Weddell seals detect novel holes in the ice at ranges where the light from the hole just exceeds their visual sensitivity threshold. A prediction of maximum sensitivity was made from laboratory results with harbor and spotted seals (Wartzok 1979). In spite of the extrapolations from laboratory data to the field situation and from harbor and spotted seals to Weddell seals, the detection distances correspond to those predicted based on the maximum sensitivity at typical states of adaptation, and on the extinction coefficients in the water column (Wartzok et al. 1992).

The fact that the pupils of marine mammals are usually constricted when they are in bright light at the surface is one factor that helps prevent a total bleaching of the rod pigment. The constricted pupil not only helps preserve a partial state of dark adaptation, it is also essential for visual acuity in air.

Visual Acuity

Visual acuity is a measure of how well an animal can resolve features in its visual environment. For example, it can be measured by determining how far apart two points of light must be for the subject to detect that there really are two lights, rather than one; or how broad alternating stripes of black and white must be for the subject to recognize them as stripes, rather than a uniform gray. Because these separations of lights or widths of stripes varies with distance from the subject, visual acuity is usually measured in terms of degrees or minutes of arc. As a point of reference, the diameter of the full moon is about one-half degree, or 30 min of arc. Visual acuity is dependent on the focusing ability of the optics of the eye, the density of receptors in the retina, the connections between the receptors, and the subsequent processing of the signal in the central nervous system.

The extent to which light rays are refracted when they pass through the interface between different media is dependent on the difference in refractive indices of the media and the angle of the light with respect to the interface be-

tween the media. If the light ray is perpendicular to the interface, the ray is not refracted. The strength of a homogeneous lens in air, therefore, is dependent on its refractive index and its radius of curvature. A light ray entering a terrestrial eye experiences its greatest difference in refractive index at the air–cornea interface (Fig. 4-11). Depending on the radius of curvature, this can produce a lens with a strength of 25 to 40 diopters. Diopters are a measure of the refractive power of a lens given as the reciprocal of the focal length in meters. In humans, focusing at the air–cornea interface accounts for about two-thirds of the total focusing power of the visual system. The actual lens within the eye provides only about one-third of the focusing power. When terrestrial mammals returned to the sea, they had to compensate for the loss of a major focusing element in their visual systems. The reason they lost the cornea interface lens power is that the refractive index of water is similar to that of the interior of the eye, therefore there is little change in refractive index as light passes from the water into the eye through the thin cornea. To see well underwater, marine mammals have developed much stronger lenses. Refractive measurements of the eyes of several species have shown that they are approximately emmetropic, neither near- nor far-sighted, for underwater vision (bottlenose dolphin: Dawson et al. 1972, Dral 1972; harbor seal: Johnson 1893; harp seal: Piggins 1970; Weddell seal: Wilson 1970).

The lenses in marine mammal eyes are more similar to those in fish eyes than they are to the lenses in terrestrial mammalian eyes. In cetaceans, the lenses are spherical in shape and the ciliary muscles that change the shape of the lens for accommodation, or focusing, appear to be nonexistent (Dral 1972). In pinnipeds, the lenses have a shape intermediate between those of cetaceans and terrestrial mammals, and ciliary muscles are attached to the sclera, an

arrangement that has been postulated to allow for a strong pull on the thick lens (Jamieson and Fisher 1974).

The strong lens that compensates for the loss of the air–cornea interface when the animal is underwater leads to severe myopia when the animal is out of the water and regains the air–cornea lens. Exactly how marine mammals overcome myopia in air is not well understood. One way is through extensive pupillary contraction to a slit that can close further to form a pin hole. The slit is oriented vertically in the majority of pinnipeds, and horizontally in cetaceans, and in bottlenose dolphins it takes the shape of a horizontal crescent that closes to two slits at the ends of the crescent (a double slit pupil) (Herman et al. 1975, Dawson et al. 1979). A pin hole camera approaches an infinite depth of field so an eye with a pin hole pupil will be emmetropic and an eye with a slit pupil could provide focused images over a range of distances.

The constricted pupil works well for animals in bright light, but as the light intensity decreases and the pupil opens, visual acuity declines. Schusterman and Balliet (1971) compared visual acuity in California sea lions above and below water as the illumination decreased (Fig. 4-12), and demonstrated that performance degraded much more rapidly in air than underwater. The initial good visual acuity in air is also attributable to an apparently unique feature of the cornea of California sea lions (although no other otariids have been carefully studied). In the center of the cornea there is a 6.6-mm diameter circular flattened area (Dawson et al. 1987b). Because this portion of the cornea has no curvature, it does not act as an additional lens in the air, and the sea lion has equivalent aerial and underwater vision as long as the pupil does not dilate beyond this diameter.

Although the above considerations certainly contribute to functional vision in air, a few problems are not fully ex-

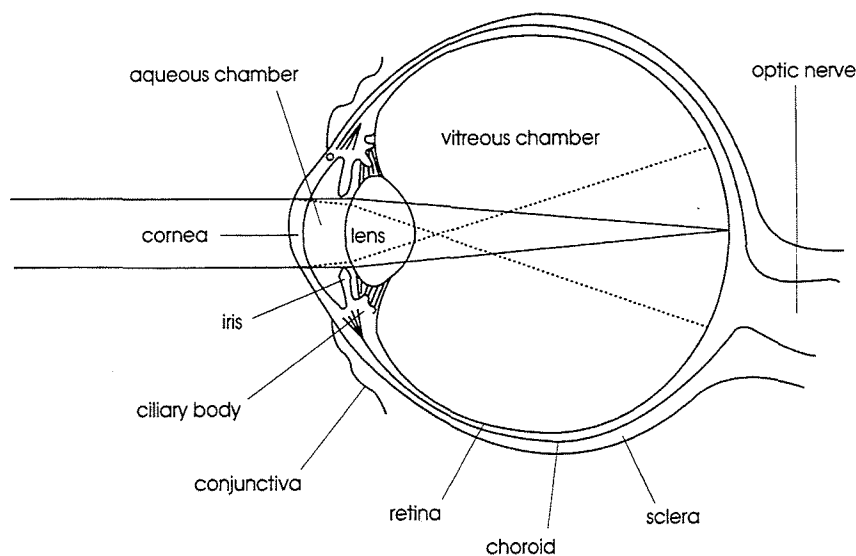


Figure 4-11. Ray drawings of the focusing of a seal's eye in air and underwater. Underwater (solid line rays) there is no refraction at the cornea. The only refraction occurs at the lens. When in air, there is bending of the light at both the cornea and at the lens leading to focusing well in front of the retina (i.e., myopia). The bending at the lens is exaggerated to clearly show the effect.

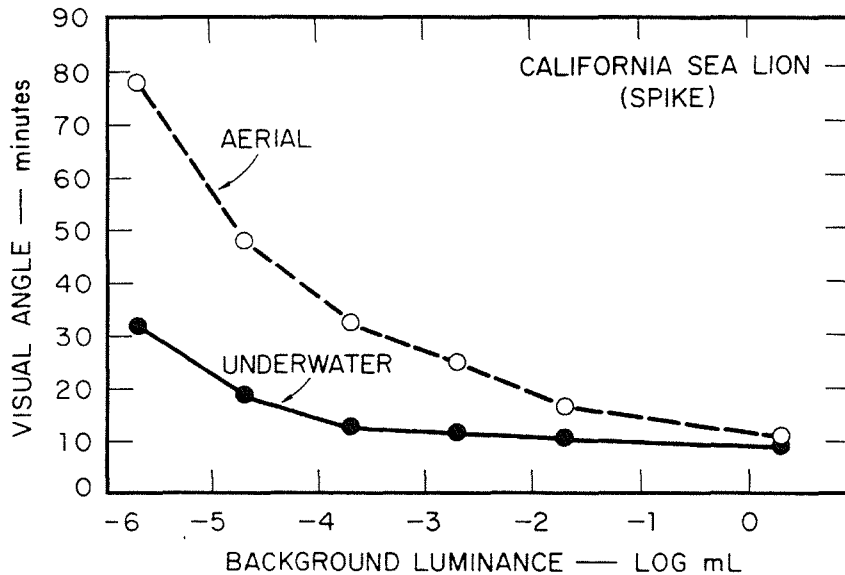


Figure 4-12. Aerial and underwater visual acuity thresholds as a function of luminance. (Reprinted from Schusterman and Balliet 1971, ©New York Academy of Sciences.)

plained. First, Dawson et al. (1979) showed that the time course of pupillary constriction is too slow to allow a bottlenose dolphin to constrict its pupil between the time its head leaves the water on a leap and the time at which it has to make the final trajectory correction before its flukes leave the water. Nevertheless, dolphins can leap accurately to targets placed at variable locations above the surface. Rivamonte (1976) argued that the double slit pupil becomes diffraction limited before the pupil has constricted sufficiently to achieve the acuities reported in air (Herman et al. 1975), and he proposed that the dolphin has a lens that overcorrects for spherical aberration by having the central core of the lens surrounded by a region of lower refractive index. Light passing through the periphery of the lens (i.e., coming from the peripheral field of view), would need the additional strength of the air–cornea interface to focus, and thus would be out of focus underwater, whereas light passing through the lens on axis would be in focus underwater but out of focus in air. There is behavioral evidence that dolphins preferentially use peripheral areas of the retina for forming images in air (Dawson et al. 1972, Pepper and Simmons 1973, Dral 1975).

Two areas of high ganglion cell density are found in the retinas of the following species: bottlenose dolphin (Dral 1975, Mass and Supin 1995); the common dolphin (*Delphinus delphis*) (Dral 1983); the finless porpoise (*Neophocaena phocaenoides*), and the Chinese river dolphin (*Lipotes vexillifer*) (Gao and Zhou 1987); harbor porpoise and gray whale (Mass and Supin 1990, 1997); and Dall's porpoise and minke whales (Murayama et al. 1992). A rostral high-density area could improve vision to the side, whereas a dorsotemporal high-density area could improve frontal vision. However, the peak densities of ganglion cells (500 to 670/mm² in bottlenose dolphins, Dral 1977, Mass and Supin 1995) are well

below the peak densities in rabbits (10,000/mm², Rodieck 1973) and cats (4,000/mm², Stone 1965). Mass and Supin (1995) calculate that the cell densities in bottlenose dolphins would limit the retinal resolution to about 9 min of arc underwater and 12 min of arc in air.

Kröger and Kirschfeld (1994) showed that the cornea, rather than being a thin membrane that does not add an optical element to the visual pathway, can be a negative lens for images formed in the periphery of the visual field. Kröger and Kirschfeld (1992, 1994) measured the variable thickness and refractive index of the cornea in harbor porpoises, and argued that the negative corneal lens was required to compensate for a too powerful positive lens in the eye of the porpoise to produce emmetropia for underwater viewing. The same arrangement could help alleviate myopia in air.

Visual acuities of cetaceans and pinnipeds fall in the range of 5 to 9 min of arc both for underwater vision and for in-air vision at high light intensities (Schusterman and Balliet 1970a,b, 1971; White et al. 1971; Herman et al. 1975). These values are similar to those reported for terrestrial hunters such as the cat (Muir and Mitchell 1973).

Sirenians

Sirenians have been reported to have poor vision (Walls 1942), based on early studies of manatees (e.g., Chapman 1875) and dugongs (e.g., Petit and Rochon-Duvigneaud 1929). These studies suggested poor visual acuity both in air and underwater with probably an exclusively rod retina, but no tapetum. On the basis of observations of manatee visual behavior, Hartman (1979) suggested they were not as visually deficient as the older literature indicated. More recent studies (Cohen et al. 1982) indicated that the manatee has both rods and cones in its retina with a central visual area

where visual acuity may be enhanced. Although there is little refractive error in the optics of the eye underwater (Piggins et al. 1983), acuity is still considered to be only moderate. The rod-dominated retina, with extensive summing of receptors to ganglion cells, indicates that acuity has been sacrificed for vision at low light levels in murky water, but the lack of a tapetum indicates a less than full adaptation to functioning at these light levels.

Ursids

Polar bears show little adaptation for underwater vision. With the loss of the air–cornea interface, the polar bear loses more than 20 diopters of lens strength underwater (Sivak and Piggins 1975). The peak sensitivity of the dark-adapted eye is at 525 nm, even a bit longer wavelength than typical of terrestrial predators such as the cat. The polar bear has both rods and cones in its retina as indicated by separate scotopic (i.e., dark adapted) and photopic (i.e., light adapted) functions (Ronald and Lee 1981).

Fissipeds

The sea otter has the most spectacular accommodative range of any vertebrate. It is able to see well in air and in water by a unique method of changing the radius of curvature, and hence the strength, of its lens (Murphy et al. 1990). As shown in Figure 4-13, when the sea otter is underwater, the loss of the approximately 60 diopter corneal–air interface lens is compensated for by the action of the ciliary and iris muscles. The ciliary muscle opens a path for fluid to flow from the anterior chamber into the corneoscleral venous plexus. This reduces the pressure in the anterior chamber and causes the lens to be pushed forward by the pressure differential between the posterior and anterior chambers. As

the lens is pushed forward, the iris sphincter forces it to assume a new shape with a much smaller radius of curvature, increasing the strength of the lens by 60 diopters. Although the iris does not close to a slit or pin hole, as in dolphins and seals, because the accommodative mechanism is dependent on the iris muscle, there is the same trade off between sensitivity in low light and visual acuity. Although no behavioral studies have been done on sea otter acuity and light levels, Schusterman and Barrett (1973) showed that an Asian “clawless” otter (*Amblonyx cineria cineria*) lost acuity underwater more rapidly than in air when light levels decreased.

Chemoreception

Both air and water are fluids; therefore, the underlying principles of the spread of chemicals through diffusion and convection in laminar and turbulent flow are the same. However, diffusion is approximately 10,000 times slower in water than in air and average water currents are approximately 15 times slower than average air currents (Vogel 1981). Thus, some aspects of chemical communication in water are far less efficient than chemical communication in air.

Smell and taste are closely aligned senses for detection of substances in air and in liquids, respectively. Neither sensory modality has been investigated with much rigor in marine mammals. Olfactory sensation appears to decline in parallel with adaptation to the marine environment. Gustatory sensation is present in dolphins, and presumably in other marine mammals, but there is a paucity of experimental evidence. The difficulty of controlling, measuring, and presenting chemical stimuli, as well as the limited availability of marine mammals for experiments, results in very slow progress in this area. Lowell and Flanigan (1980), Watkins and Wartzok

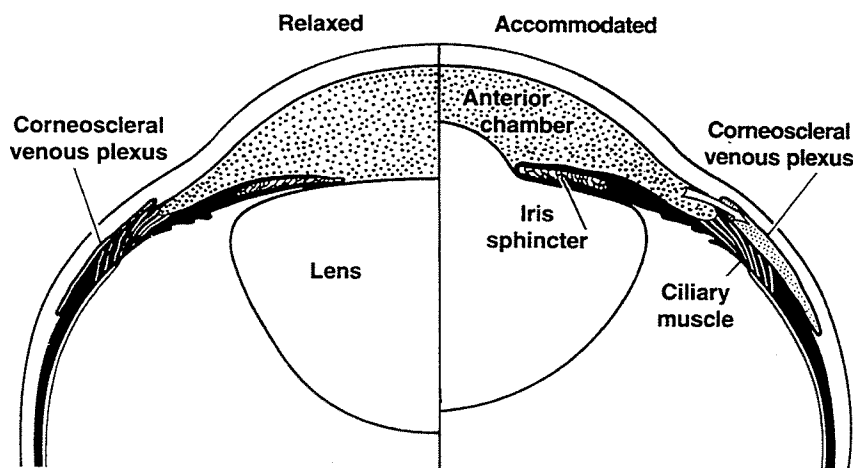


Figure 4-13. Proposed mechanism of visual accommodation for underwater vision in the sea otter. In this model, the ciliary and iridal muscles act to decrease markedly the radius of curvature of the anterior lens surface, thus making a stronger lens to compensate for the loss of the air–corneal interface lens. Contraction of the ciliary muscle will bring about a dilation of the corneoscleral venous plexus, lowering its hydrostatic pressure and causing redistribution of aqueous humor from the anterior chamber into the plexus (arrow). This pressure will bring about an anteriorward movement of the lens which is then deformed by action of the iris sphincter muscle. (Reprinted from Murphy et al. 1990, ©Elsevier Science Inc.)

(1985), and Nachtigall (1986) have reviewed basically the same small set of experimental results.

Olfaction

Anatomically, the olfactory system of mysticetes, odontocetes, and sirenians is less developed than those of terrestrial mammals. Odontocetes lack olfactory bulbs and attendant ganglia or fiber tracts (Breathnach 1960, Pilleri and Gihl 1970, Morgane and Jacobs 1972). Manatees have a very rudimentary olfactory system, and, like cetaceans, lack an important component of the olfactory system, a vomeronasal organ (Mackay-Sim et al. 1985). Pinnipeds have both peripheral (Kuzin and Sobolevsky 1976) and central (Harrison and Kooyman 1968) olfactory structures, although in phocids and walrus they are somewhat reduced compared to those of otariids (Harrison and Kooyman 1968). Both otariids and phocids show behavioral evidence of olfactory sensation. Among many examples that could be cited, males sniff the hindquarters of females to assess the state of estrus in northern fur seals (*Callorhinus ursinus*) (Bartholomew 1953) and South African fur seals (*Arctocephalus pusillus*) (Rand 1955). In southern elephant seals, experienced females begin smelling a newborn pup sooner after birth than do primiparous females (McCann 1982), and learn the identity of their pups sooner.

Gustation

Neuroanatomy (Jacobs et al. 1971) and tongue morphology (Sukhovskaya 1972, Donaldson 1977, Yamasaki et al. 1978) indicate that odontocetes have the ability to taste. Jacobs et al. (1971) suggested that the well-developed olfactory lobes in the rhinencephalon of bottlenose dolphins might be innervated by the trigeminal nerve, in place of the missing olfactory nerve, and thus might be sensitive to substances stimulating receptors on the tongue. Taste buds located in grooves or pits at the root of the tongue have been described in bottlenose dolphins (Sukhovskaya 1972, Donaldson 1977), common dolphins (Sukhovskaya 1972), and the striped dolphin (*Stenella coeruleoalba*) (Yamasaki et al. 1978, Komatsu and Yamasaki 1980). In manatees, taste buds are located in dorsal and posterior lateral swellings on the tongue (Yamasaki et al. 1980). In dugongs, the taste buds are located in pits rather than swellings in the same general dorsal and posterior lateral areas of the tongue (Yamasaki et al. 1980). Although the number of gustatory receptors is greater in sirenians than in cetaceans, they are still poorly endowed compared to herbivorous land mammals.

Kuznetsov and colleagues, using a number of different

behavioral and physiological indicators, have reported chemoreception for a number of substances (for review, see Kuznetsov 1990). These studies showed that harbor porpoise, common dolphin, and the Black Sea bottlenose dolphin could detect a variety of chemicals with a well-developed ability to detect bitter chemicals, a less well-developed ability to detect salinity, and an apparent inability to detect sugar. None of the experiments determined detection thresholds by comparing differing response levels with different stimulus concentrations.

Nachtigall and Hall (1984) used a go/no-go operant conditioning technique with a bottlenose dolphin to establish detection thresholds for sour (citric acid), bitter (quinine sulfate), salt, and sweet (sucrose). They showed that the dolphin could detect tastes humans classify as sour and bitter at levels only slightly above the range of human detection thresholds. In contrast to the results of Kuznetsov (1979), the dolphin used by Nachtigall and Hall was able to detect sucrose, although at much higher thresholds than those of humans. Nachtigall and Hall (1984) also showed a sensitivity to salt, but these results were confounded by the animal being held in salt water. In summary, the results show that dolphins with taste receptors located only at the root of the tongue can detect chemicals assigned by humans to all four of the taste groups.

Little work has been done on taste sensation in pinnipeds. Kuznetsov (1982, cited in Friedl et al. 1990) reported that Steller sea lions (*Eumetopias jubatus*) detected sour, bitter, and salty stimuli, but were insensitive to sweet. Friedl et al. (1990) reported on experiments done with a California sea lion using the same techniques used by Nachtigall and Hall (1984). The sea lion was good at detecting citric acid, and discriminated between freshwater and seawater, but had a high threshold for bitter, and appeared not to detect sweet. As Friedl et al. (1990) noted, "much work remains for patient researchers in the area of marine mammal chemoreception."

Tactile Sensation

Cetaceans

Most of the studies of tactile sensation in cetaceans have been done in bottlenose dolphins with the objective to understand how these animals maintain laminar flow over major portions of the body at fast swimming speeds. Gray's paradox (Gray 1936) suggested that dolphin muscles would need to be seven times more powerful than they are if the dolphin experienced the turbulent flow predicted by their body shape and speed of movement through the water. Lang and co-workers (Lang 1966, Lang and Norris 1966, Lang and Pryor

1966) demonstrated that for several odontocetes drag coefficients measured during glides were indicative of turbulent flow over the entire surface of the animal. They suggested that energetically problematic high-speed swimming was limited to short bouts so that reasonable estimates of propulsive power capabilities were not violated. However, drag measured during a glide is not necessarily representative of drag during active swimming (Alexander and Goldspink 1977). If the animals are capable of actively damping turbulence, they could likewise be capable of not damping it or enhancing it based on their intention to move forward or glide to a stop. Support for some form of active damping comes from observations showing that little turbulence is generated over most of the body of a swimming Pacific white-sided dolphin. A number of investigators have speculated, based on the anatomy of the skin and the innervation of the skin, that active damping of incipient turbulence is occurring (Kramer 1965, Surkina 1971, Kayan 1974, Khomenko and Khadzhinskiy 1974, Babenko and Nikishova 1976, Ridgway and Carder 1990).

The first step in determining whether dolphins are capable of active damping is to assess their tactile sensitivity. Kolchin and Bel'kovich (1973) used galvanic skin responses to map areas of greatest sensitivity on the body of common dolphins. They found the area of highest sensitivity within 2.5 cm from the blowhole and in separate 5-cm diameter circles around the eyes. The next most sensitive area was the snout, lower jaw, and melon. The area of the back, both anterior and posterior to the dorsal fin, had a lower sensitivity. Bryden and Molyneux (1986) found large numbers of encapsulated nerve endings in the region of the blowhole in both bottlenose dolphins and false killer whales. They suggested

that these mechanoreceptors were involved in detection of the pressure changes associated with the blowhole breaking the water surface. They found more receptors on the anterior lip of the blowhole, the first part of the blowhole that would become exposed when the animal surfaced. These most sensitive areas are not the most critical areas for dampening turbulence.

Using electroencephalograms to map areas of tactile sensitivity on the body of bottlenose dolphins, Ridgway and Carder (1990) expanded on early studies by Lende and Welker (1972). They found highest sensitivity at the angle of the gape, followed by the area around the eyes and melon, followed by the area around the tip of the snout and the blowhole. The least sensitive areas were on the remainder of the dolphin's trunk. Although there are some differences in most sensitive areas, the results of Ridgway and Carder (1990) and Kolchin and Bel'kovich (1973) agree that the head region is the most sensitive. The minimum detectable pressure values of 10 mg/mm², obtained by Kolchin and Bel'kovich (1973) using a static, weighted 0.3-mm wire, are similar to those obtained for humans in their most sensitive areas such as the fingertips and lips. Even the 40 mg/mm² found on the common dolphin trunk shows a high level of tactile sensitivity over the majority of the body.

Knowing a dolphin is capable of detecting pressure associated with turbulence as it swims is only part of the issue of whether a dolphin can actively damp turbulence. To determine whether there is muscle control sufficient to effect the damping, Haider and Lindsley (1964) and Ridgway and Carder (1990) studied microvibrations in bottlenose dolphins. Haider and Lindsley (1964) showed that these vibrations were at least three times greater in amplitude in

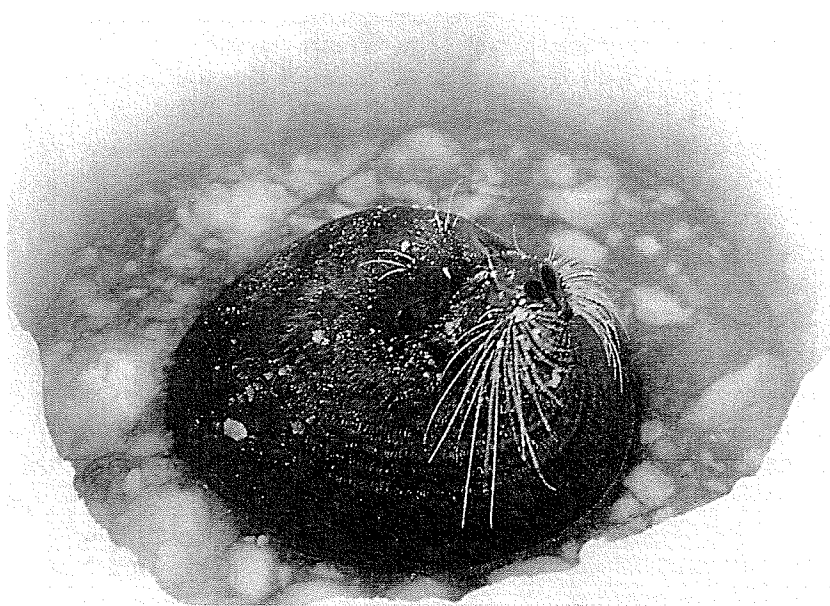


Figure 4-14. A photograph of a ringed seal surfacing through a manmade hole in the ice. The extensively developed vibrissae are obvious.