Why pinnipeds don't echolocate

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Odontocete cetaceans have evolved a highly advanced system of active biosonar. It has been hypothesized that other groups of marine animals, such as the pinnipeds, possess analogous sound production, reception, and processing mechanisms that allow for underwater orientation using active echolocation. Despite sporadic investigation over the past 30 years, the accumulated evidence in favor of the pinniped echolocation hypothesis is unconvincing. We argue that an advanced echolocation system is unlikely to have evolved in pinnipeds primarily because of constraints imposed by the obligate amphibious functioning of the pinniped auditory system. As a result of these constraints, pinnipeds have not developed highly acute, aquatic, high frequency sound production or reception systems required for underwater echolocation. Instead, it appears that pinnipeds have evolved enhanced visual, tactile, and passive listening skills. The evolutionary refinement of alternative sensory systems allows pinnipeds to effectively forage, navigate, and avoid predators under water despite the lack of active biosonar capabilities. © *2000 Acoustical Society of America.* [S0001-4966(00)01804-X]

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INTRODUCTION

The most recent review of dolphin echolocation (Au, 1993) clearly shows that these animals have evolved sophisticated sonar systems to explore their environment. Echolocation performance depends on the evolution of specialized sound production, sound reception, and signal processing mechanisms. Active biosonar has enhanced the ability of odontocete cetaceans (dolphins and other toothed whales) to exploit underwater foraging environments where the visual sense is often of limited use. For this reason, echolocation has periodically been hypothesized to occur in other marine mammals, specifically the pinnipeds (seals, sea lions, and walruses).

Echolocation in bottlenose dolphins (*Tursiops truncatus*) was convincingly demonstrated about 40 years ago in experiments that required echolocating dolphins to perform obstacle avoidance or object discrimination tasks (Schevill and Lawrence, 1956; Kellogg 1958; Turner and Norris, 1966). To ensure that the dolphins were relying on biosonar and not visual cues while performing these operations, the dolphins completed the experimental tasks while swimming in murky or dark waters or while wearing rubber suction cups over their eyes (Schusterman, 1980). These subjects were able to orient in darkness by using a bistatic, active sonar system employing high frequency sounds. This system is used by many, if not all, odontocetes to detect and avoid obstacles and pursue prey. High frequency biosonar is selectively advantageous because of the increased resolving power of a system using signals with wavelengths smaller than the objects being targeted. This is especially important in water, in which sound speed is greater than sound speed in air by a factor of more than 4.

Like dolphins, pinnipeds forage at times in relatively dark waters. This ecological similarity eventually led to the proposition that most, if not all, pinnipeds had also evolved specialized sound emissions and hearing abilities in order to echolocate (Poulter, 1963). Indeed, Poulter (1963, 1966, 1967) reported that he had experimentally demonstrated sophisticated echolocation in California sea lions (*Zalophus californianus*) following observations and underwater recordings of captive animals approaching food items under a variety of conditions. Poulter (1967) additionally suggested that other otariid pinnipeds including the Steller sea lion (*Eumetopias jubatus*) and the northern fur seal (*Callorhinus ursinus*) used their normal in-air vocalizations for underwater echolocation signals. However, contrary to Poulter's (1963) observation that California sea lion underwater vocalizations ranged in frequency from 5 to 13 kHz while approaching fish in the dark, other investigators found that most of these sounds were of low frequency (<4 kHz), and were associated with social interactions rather than foraging activity (Schevill *et al.*, 1963; Schusterman, 1967). Systematic experimentation on the sonar ability of California sea lions has consistently yielded negative results (Evans and Haugen, 1963; Schusterman, 1967).

Poulter (1967) also hypothesized that some of the phocid seals, including bearded seals (*Erignathus barbatus*), Weddell seals (*Leptonychotes weddellii*), and leopard seals (*Hydrurga leptonyx*) had evolved highly specialized sonar systems. In contrast to the otariids, which vocalize under water somewhat infrequently, most phocids routinely emit underwater signals that are thought to be related primarily to reproductive behavior. With few exceptions, these sounds are low in frequency (see Richardson *et al.*, 1995, for a review). Renouf and Davis (1982) hypothesized that the pulsatile sounds produced by harbor seals (*Phoca vitulina*) constitute active biosonar signals; however, their interpretations of a target discrimination experiment on this species were challenged based on alternative explanations for the seal's performance (Wartzok *et al.*, 1984). Other experiments testing for echolocation in phocids have been performed on gray seals (*Halichoerus grypus*) in controlled obstacle avoidance, maze learning, or target detection tasks. These experiments yielded negative results (Oliver, 1978; Scronce and Ridgway, 1980).

Despite the lack of supporting evidence, the pinniped echolocation hypothesis maintains a foothold in popular treatments of marine mammal acoustics, and has recently been resurrected based on earlier underwater observations on a single captive leopard seal that emitted high frequency signals while chasing fish under darkened conditions (Thomas *et al.*, 1983). The descriptions of the signals, along with the seal's behavior, have been expanded and updated (Awbrey *et al.*, in press). Awbrey *et al.* (in press), have joined Poulter (1967) in suggesting that Antarctic pinnipeds, which inhabit ice-covered areas and live in relative darkness during part of the year, are the most likely pinniped species to have evolved a specialized echolocation system, and that a variety of acoustic signals are used by these species in contexts of foraging and navigation.

Echolocation, defined in an evolutionary sense, is a specialized adaptation and not a generalized skill that may be used fortuitously when other sensory modalities are in some way prevented from being used. Examples of opportunistic echolocation include experimental evidence that blind and sighted humans can be trained to detect, locate, and discriminate targets by listening for reflected echoes (Rice *et al.*, 1965). In addition, rats are capable of using echoes from the sounds of their own movements to facilitate navigation through a maze (Riley and Rosenzweig, 1957). However, neither humans nor rats have evolved specialized mechanisms to detect objects or navigate via echolocation, even though such performance can emerge through experience (Schusterman, 1981). Indeed, the very notion that dolphins and microchiropteran bats perform complex tasks using sophisticated active biosonar is diminished by an expanded definition of echolocation that also includes the anomalous performance of nonspecialized animals. In a general sense, even though many, if not all, higher vertebrates can learn to use echoes to gain information about their environment in a crude or rudimentary fashion, most do not possess a specialized echolocation system [but see Tyack (1997) for a counter-argument].

In this paper, we consider the issue of whether some or all species of pinnipeds possess specialized acoustical abilities for underwater echolocation of the type shown by odontocete cetaceans. We will argue that, unlike the aquatic dolphins, pinnipeds have not developed active biosonar; rather, the amphibious lifestyle of pinnipeds has resulted in relatively nonspecialized underwater hearing abilities. We propose that many pinniped species depend on sensory capabilities other than active biosonar, including underwater hearing, enhanced vision, and acute hydrodynamic reception to explore their environment, particularly while foraging.

I. EARS AND HEARING

The typical mammalian ear is adapted to hear in air. The transition of certain vertebrates from water to land was accompanied by the evolution of the middle ear as an impedance matching mechanism, allowing the originally water-adapted ear to function in air. Impedance matching between the environment and the inner ear is achieved primarily by pressure amplification due to lever action and areal ratio transformation by the middle ear ossicles. Low pressure/high particle velocity sound waves in air are transformed into high pressure/low particle velocity waves in the inner ear fluid. The adaptive radiation of some mammalian lineages into the water introduced a new air–water interface separating the liquid environment and the air-filled middle ear. The middle ear, instead of performing its normal pressure amplifying function, would have suffered a severe loss of efficiency, because nearly 100% of incident acoustic energy is reflected at the air–water interface. In order to maintain auditory sensitivity under water, secondarily aquatic vertebrates needed to develop novel auditory adaptations; consequently, aquatic ears evolved independently and to different degrees in at least three lineages of marine mammals (carnivores, cetaceans, and sirenians). Organisms in only one of these groups (the odontocete suborder of the cetacea) are known to use echolocation. In roughly 60 million years of cetacean evolution, the outer and middle ears of odontocetes have become dramatically modified to facilitate reception of waterborne sound. The precise sound routes and sensory mechanisms involved in sound detection have not been elucidated; however, it is commonly accepted that the dolphin ear has become fully water-adapted in terms of best absolute sensitivity and differences between hearing in air and in water (see Ketten, 1992, for a review of the cetacean ear). The evolutionary restructuring of the dolphin ear for underwater use was possible in part because the cetacean lineage, in contrast to the secondarily aquatic carnivore lineages, has evolved entirely in water.

The first pinnipedlike animals appear in the fossil record about 27–25 million years ago and the closest living relatives to modern pinnipeds are other arctoid carnivores, most likely the ursids and mustelids (Tedford, 1976), and the ancestral pinniped ear was probably similar to that of a generalized carnivore. Indeed, apart from the presence of a layer of distensible vascularized tissue, the pinniped middle ear possesses few characteristics that cannot be found in certain other terrestrial mammals (Repenning, 1972). In contrast to cetaceans, pinnipeds spend a significant portion of their lives on land, and must attend to airborne as well as underwater sounds. Unlike the dolphin ear, the pinniped ear appears to have been constrained during its evolution by the necessity of functioning in two acoustically dissimilar media.

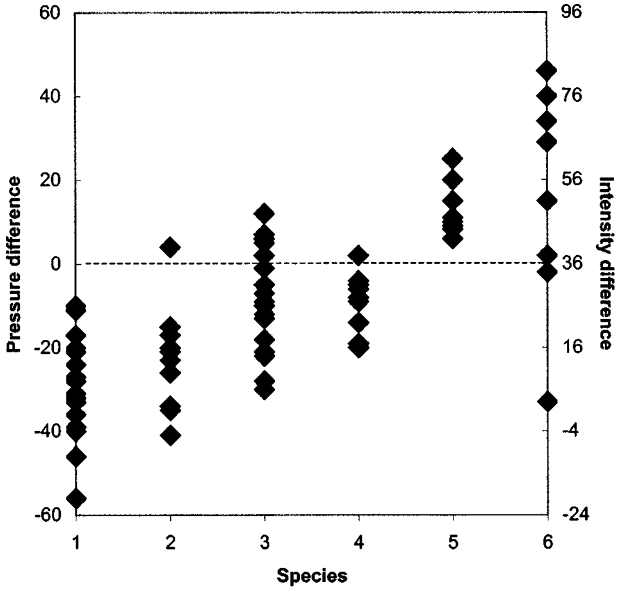

FIG. 1. Differences (in dB) between in-air and underwater sound pressure and intensity detection thresholds for five pinnipeds and one cetacean. Positive values indicate lower thresholds in water; negative values indicate lower thresholds in air. Species plotted are otariids: (1) northern fur seal, (2) California sea lion; generalized phocids: (3) harbor seal, (4) harp seal; and aquatic specialists, (5) northern elephant seal, (6) bottlenose dolphin. Statistically significant differences occur between all groupings: otariids and generalized phocids; otariids and water specialists; and generalized phocids and water specialists. Data summarized from Kastak and Schusterman (1998, 1999) and Richardson *et al.* (1995).

Early interpretations of amphibious functioning indicated that the seal ear was intermediate between a water adapted and an air adapted ear, given that a fully water-adapted ear would suffer a 30-dB loss in sensitivity in air and vice versa (Møhl, 1968). Later audiometric studies showed that, in general, the phocids appeared to be semi- or fully water adapted while the otariids, though able to hear with greater sensitivity under water than in air, did so with less facility than the phocids [see reviews by Schusterman (1981) and Richardson *et al.* (1995)]. In terms of the detection of acoustic energy, all pinnipeds tested thus far hear better in water than in air. However, in terms of acoustic pressure detection, the otariids appear to be primarily adapted to hear in air, while the phocids are generally adapted for amphibious hearing (Kastak and Schusterman, 1998). This trend holds for all phocids thus far studied except the deep-diving northern elephant seal, which detects acoustic pressure better under water than in air (Kastak and Schusterman, 1999). In Fig. 1, we demonstrate that the northern elephant seal shows differences in aerial and underwater sensitivity paralleling those of the bottlenose dolphin, implying aquatic specialization. The figure also shows that when pairwise comparisons of air–water sensitivity are made between pinnipeds, there are significant differences between phocids and otariids, and between the elephant seal and all other pinnipeds whose hearing has been tested both in air and under water. The patterns of air and water hearing sensitivity appear to correspond to the patterns of the life history of three pinniped assemblages: the otariids, the generalized phocids (*Phoca spp.*), and the northern elephant seal, a specialized phocid (Kastak and Schusterman, 1998, 1999). Except for the elephant seal, the pinnipeds have retained good airborne hearing sensitivity, and the necessity to hear well in air has constrained the development of the exceptional underwater sensitivity necessary for refined echolocation. However, even the elephant seal (in contrast to the dolphin) must detect conspecific signals in air in contexts related to social behavior and pup attendance (Kastak and Schusterman, 1999).

The refinement in the pinnipeds of sensory mechanisms other than echolocation for underwater orientation was due in part to selection pressures for maintaining auditory sensitivity in air, but also to phylogenetic constraints of the basic carnivore ear structure. These constraints are illustrated by a comparison between the aerial hearing sensitivity of the generalist pinnipeds and terrestrial carnivores. These taxa are similar in terms of best sensitivity (no more than 10–20 dB difference between pinnipeds and most nonfeline carnivores tested) and in terms of upper frequency limit (no more than 10–15 kHz difference between pinnipeds and most nonfeline carnivores; Fay, 1988). Differences in best sensitivity can be accounted for by the structure of the pinniped external meatus, which acts as a valve to keep water from entering the ear upon submersion. Differences in upper frequency limit of pinnipeds and fissipeds may be related to differences in body size (Rosowski, 1994). The conservation of the basic carnivore ear is evident not only in anatomy (Repenning, 1972) but in aerial function as well (e.g., Moore and Schusterman, 1987). Based on these factors, it is likely that both phylogenetic constraints and selective pressures acting to maintain airborne sensitivity precluded the development of very acute high frequency sensitivity necessary for efficient echolocation in the aquatic environment. The pinniped ear has instead evolved through natural selection to function amphibiously, perhaps at the cost of the evolution of an active biosonar system.

II. PASSIVE BIOSONAR

Laboratory experiments have shown that both phocid and otariid pinnipeds can localize underwater signals of low and intermediate frequencies up to about 16 kHz (reviewed by Schusterman, 1981) and therefore, by listening, may obtain a wealth of biologically significant information from their underwater environment. In addition to determining the location and status of conspecifics, certain pinnipeds may acoustically detect and localize predators such as sharks and killer whales. Sharks produce no communicative acoustic signals, but incidental sounds associated with their swimming or feeding may alert nearby pinnipeds. Killer whales do emit social and echolocation signals and there is some evidence suggestive of the ability of pinnipeds to detect them. A population of mammal-hunting killer whales in the north Pacific echolocate with fewer, more irregularly spaced clicks compared to another population that forages on fish (Barrett-Lennard *et al.*, 1996). These killer whale echolocation clicks have significant energy from 4 to 18 kHz, a span that falls within the most sensitive hearing range of most pinnipeds but is above the upper frequency hearing limit of most fish species (Popper and Fay, 1993). These observations are augmented by a report that killer whales in the

Indian Ocean are also acoustically cryptic when preying on southern elephant seals and king penguins (Guinet, 1992). In a captive setting, Schusterman and Kastak (1996) found that a northern elephant seal failed to habituate to, and in fact became sensitized to pulsatile sounds resembling killer whale echolocation clicks. These observations indicate that underwater hearing may play an important predator alerting function for the pelagic deep diving elephant seals that must spend more time resting at sea than more coastal species. This predator–prey system is analogous to the coevolution of the echolocation signals of some insectivorous bats and their detection by nocturnal moths (Fenton and Fullard, 1981).

Localization of prey by the sounds they produce may be an additional use of underwater hearing. Acoustic signals are produced under water by a wide range of organisms preyed upon by pinnipeds. Swimming, struggling, or foraging animals produce incidental sounds that may attract predators (Myrberg, 1981). Additionally, many invertebrates, teleost fish, and other marine animals produce communicative sounds in social, reproductive, and foraging contexts that may be detected over greater distances (Tyack, 1998). Interception of prey sounds by predators has been documented in several fish species (see Myrberg, 1981), and some cetaceans have been shown to acoustically detect prey items without using echolocation when they are experimentally blindfolded or are too far from prey for visual detection (Wood and Evans, 1980; Barrett-Lennard *et al.*, 1996). It is not known whether pinnipeds can detect prey by eavesdropping on the sounds they make; however, captive California sea lions can locate live fish, without emitting sound, in conditions of limited visibility (Schusterman, 1967). These findings may help to explain observations of apparently blind, free-ranging pinnipeds that survived for relatively long periods, thus supporting the notion that their hearing plays some role in prey detection (Schusterman, 1981).

In addition to facilitating predator avoidance and prey capture, hearing in pinnipeds may also function in spatial orientation and navigation. Many pinnipeds are active at night or in turbid water where vision is of reduced utility as an orientation mechanism. Others spend long periods diving deeply and continuously at sea where visual reference to coastal, bathymetric, and celestial features is limited. Efficient propagation of acoustic signals in water has prompted speculation by Norris (1967) that sounds produced by biotic or abiotic sources may function as a guidance mechanism for pinnipeds (for example, distant wave noise may demarcate the approximate location of a coastline). In the same vein, Norris (1967) suggested that sounds produced by marine animals characteristic of specific environments might convey depth as well as ecological information to an experienced passive listener.

The function of underwater hearing in free-ranging pinnipeds remains largely uninvestigated. However, experiments in the field by Wartzok *et al.* (1992) showed that blindfolded polar seals—ringed seals (*Phoca hispida*) and Weddell seals (*Leptonychotes weddellii*)—use acoustic cues provided by the experimenters to find novel holes cut through the ice. After these seals have oriented in the presence of acoustic cues, they rapidly acquire a cognitive spatial map of their environment that allows them to navigate under the ice in the absence of these acoustic cues. Based on the observation that these seals do not vocalize while searching for holes in the ice, echolocation is apparently neither required nor used for this task.

Hearing efficiency in a noisy environment depends on the ability to detect signals embedded in noise. Masking of biologically significant sounds reduces the range over which detection may occur. Some pinnipeds vocalize incessantly during the breeding season, presumably to increase the probability of signals being detected over high levels of noise common in coastal environments (Peterson and Bartholomew, 1969; Schusterman, 1978). Based on evidence from auditory masking experiments, pinnipeds perform quite well at extracting tonal signals from noise over a range of frequencies (reviewed in Richardson *et al.*, 1995; Southall *et al.*, 1998). This is likely a result of the naturally noisy environments they inhabit and the relatively wide bandwidths of biologically significant signals they must detect, which place a premium on efficient listening. The refinement of these listening skills in the pinnipeds may have at least partially offset the pressures to develop more sophisticated active biosonar.

III. SOUND PRODUCTION

Pinnipeds produce a wide variety of signals under water, including whines, grunts, roars, chirps, and pulsed sounds (reviewed by Richardson *et al.*, 1995). Many of these sounds are known to be related to social behavior and reproduction; however, the emission of high frequency and pulsed sounds has led some researchers to speculate about the existence of echolocation in pinnipeds. In this section, we outline the characteristics of dolphin echolocation sounds (reviewed by Au, 1993) and their presumed counterparts in pinnipeds, and argue that there is at present no evidence that pulsed and/or ultrasonic pinniped sounds are used for echolocation.

The bottlenose dolphin produces broadband echolocation clicks with significant energy at frequencies above 90 kHz. The clicks are extremely loud, with source pressure levels typically exceeding 200 $\mathrm{dB}_{(pp)}$ *re*: 1 μPa. The production of loud signals probably compensates for signal and echo losses associated with sound absorption by water. The melon, a mass of fatty tissue located anterior to the braincase, is thought to enhance transmission of the echolocation pulse from the tissues of the head into the environment, as well as acting as a waveguide to focus the echolocation sound beam. As a result, the directionality of the transmitted pulse trains is extremely high. Dolphins exercise fine control over the temporal patterns of their echolocation signals; pulses are short (about 50–70 μs), and click intervals in detection tasks directly relate to the two-way transit time from source to target and back. Consequently, the dolphin has time to receive and process each echo before producing the next click. Dolphins approaching a target generally decrease the inter-pulse interval in proportion to the change in target range—individual pulses comprising click trains become more closely spaced as range decreases.

Given that pinnipeds also produce underwater sounds, it is a worthwhile question to ask whether these sounds could

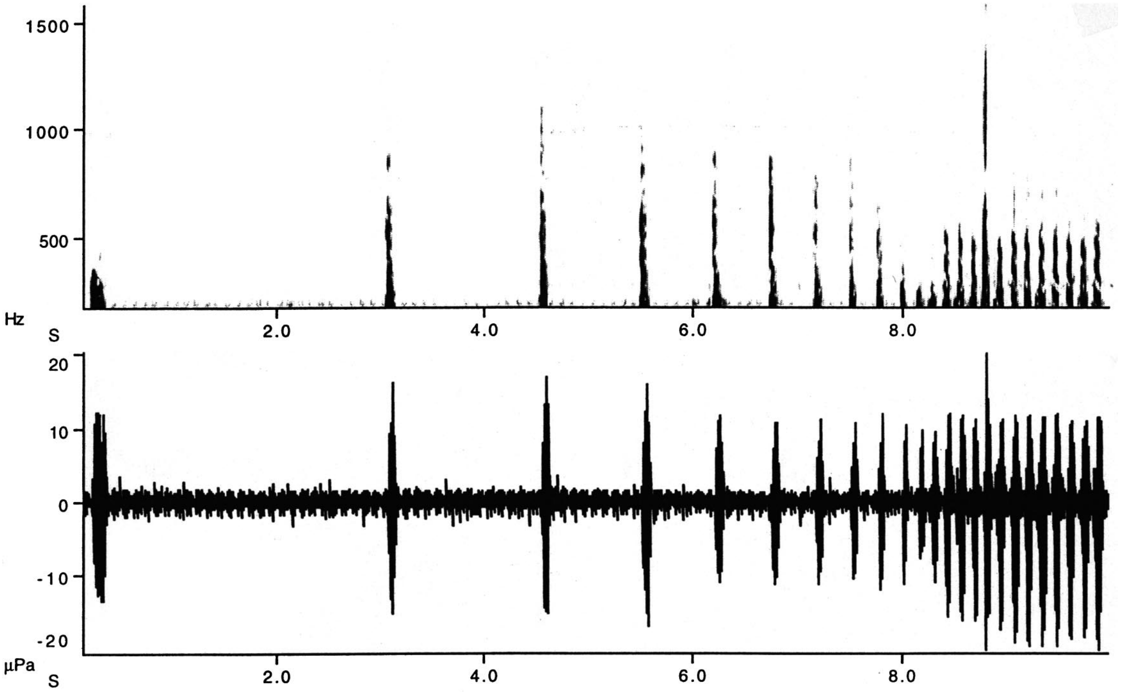

FIG. 2. Sound spectrogram and oscillogram of Weddell seal vocalizations produced while approaching an ice hole. The recording hydrophone was mounted on the seal's back (Davis *et al.*, 1999). Note the pulsatile nature and change in interpulse interval as the seal closed in on the ice hole. This figure is courtesy of Dr. William E. Evans.

function in a manner analogous to the echolocation pulses produced by odontocetes. What are the features of these sounds that make them appealing to proponents of the echolocation hypothesis? As Fig. 2 shows, many of them are pulsatile and repetitive, thus superficially resembling the click trains produced by dolphins, while some, such as those produced by the leopard seal, are ultrasonic and ought to provide detailed information about small targets. Further, many of these sounds have been recorded during foraging or navigation. Aside from the overall lack of experimental evidence for echolocation in pinnipeds, there are several uncertainties about pinniped vocalizations that have not been addressed by echolocation proponents. First, source levels are relatively low, ranging from only about 90 to 190 dB. In fact, the source levels of ultrasonic signals produced by leopard seals, perhaps the sounds most likely to be related to echolocation, have been described as ''low amplitude'' or ''weak'' (Richardson *et al.*, 1995; Thomas *et al.*, 1983). Some of these sounds, for example, FM sweeps, are also emitted almost continuously, with a duty cycle that does not appear to allow for detection and processing of echo returns between the production of subsequent outgoing pulses. Echoes from long duration FM sweeps would also be contaminated by background reverberation (especially under ice), making detection of small targets difficult. Even the shorter-duration pulses, which can be much longer than those of dolphin clicks (0.3 to >10 ms), while allowing detection of large objects, would not allow the fine target resolution seen in odontocetes. In contrast to the dolphins, pinnipeds do not appear to modify the temporal patterning of click signals according to target range in laboratory tests of echolocation performance (Schusterman, 1967). However, Evans *et al.* (in press, and as shown in Fig. 2) report that Weddell seal pulse rates changed as the seals approached ice holes. However, these authors conclude that the changes in interpulse interval might serve functions other than echolocation, for instance, arousal or advertisement (Evans *et al.*, in press). Additionally, the only pinniped tested in a temporal integration task performed relatively poorly; Terhune (1988) found that thresholds for brief pulses in a harbor seal were some 30–40 dB higher than thresholds for long tones at the frequency of best sensitivity. In contrast, the bottlenose dolphin threshold for high frequency brief pulses is only 10–20 dB higher than thresholds for long tones. Thus although the data are limited, it appears that the bottlenose dolphin, an echolocator, is better adapted to detect very brief acoustic signals than is the harbor seal. Given that best thresholds for long pure tones in the dolphin are some 20 dB lower than the best thresholds for the seal, the latter probably does not produce signals of sufficient intensity to detect prey at all but the shortest ranges, where other senses such as vision would accomplish the same task in a less energetically costly fashion. Further, the bottlenose dolphin has been shown to have a highly directional receiving beam, with a minimum audible angle of less than 1 degree for brief clicks, effectively increasing the signal-to-noise ratio of echo returns. Minimum audible angles for clicks in pinnipeds range from about 6 degrees in a California sea lion to about 4.5 degrees for a harbor seal—five to nine times poorer than the bottlenose dolphin. All of these observations suggest an acoustic system that is qualitatively different from that of the dolphin, in terms of sound production, sound reception, and orienting behavior.

Seasonal or geographic conditions of near or total darkness have been proposed as selective forces for the development of a pinniped active biosonar system. According to this hypothesis, pinnipeds that inhabit polar regions and/or dive to extreme depths are the species most likely to echolocate. Attention has recently focused on the Antarctic leopard and Weddell seals, which are known to be extremely vocal under water (Awbrey *et al.*, in press; Evans *et al.*, in press). Although Evans *et al.* (in press) have proposed that Weddell seals echolocate in a foraging context, this proposition is contradicted in a recent study by Davis *et al.* (1999) who, on the basis of underwater observations of foraging seals, concluded that, ''. . . it seems unlikely that Weddell seals use active sonar to locate prey as some other marine mammals do (p. 995).'' Further, the primary prey items of Weddell seals, notothenioid fish (Davis *et al.*, 1999), lack swimbladders and thus scatter relatively little acoustic energy, especially at low frequencies. Given the generally low frequencies and source levels of Weddell seal calls, as well as the weak target strengths of typical prey items, it is reasonable to conclude at this time that this species is unable to detect prey using active biosonar.[1] Rather, the Weddell seal, as well as the leopard seal, probably relies mainly on vision to detect prey (Davis *et al.*, 1999).

In addition to foraging, it has been proposed that pinnipeds use active biosonar to navigate, for instance, in finding ice holes from underneath the Antarctic fast ice (Evans *et al.*, in press). However, in this study, only about half the seals produced clicks while approaching ice holes, and these authors concede that the sounds may be used as social or territorial signals broadcast to conspecifics. Although there is very little information on directionality in sound production, Schevill and Watkins (1971) concluded that the Weddell seal sound beam is directed forward and down. In order to best detect ice holes using active biosonar, these seals would have to swim and surface in an upside-down position. Considering the sensitivity of the pinniped visual system, it is far more reasonable to infer that these seals navigate by sight than by active biosonar.

So, what of the considerable circumstantial and anecdotal evidence for echolocation in seals and sea lions, such as pulsatile sounds recorded from pinnipeds in foraging or navigating contexts? Conclusions regarding the functions of such signals must by made with caution. For example, many species that produce the most intense underwater sounds produce them only in contexts related to social interactions and/or general arousal (Schusterman, 1967; Ballard and Kovacs, 1995). This makes interpretation of underwater sounds produced by a hungry animal feeding in darkness problematic—such sounds may be related to affect or motivation rather than prey detection. The influence of motivational factors on sound production in most pinnipeds is likely to remain unknown until more data on the underwater behavior of these animals are available. Until we gain a comprehensive picture of the sensory systems of species such as the Weddell and leopard seals, echolocation cannot be completely ruled out as a possibility. On the other hand, given the relative ease with which echolocation can be examined in many odontocetes, it is improbable that this ability is merely being overlooked in the pinnipeds.

IV. VISION

In the majority of reviews of pinniped sensory ecology, hearing is assumed to be of paramount importance to underwater foraging and navigation. Reliance on the acoustic sense seems to be a straightforward proposition, given the relative efficiency with which sound waves propagate under water. Light, on the other hand, is absorbed rapidly in the water column, and it is often assumed that complete or nearly complete darkness is characteristic of marine mammal foraging environments. However, a few authors (e.g., Schusterman, 1981) have attempted to reinforce the idea that pinnipeds forage visually, based on studies of anatomy (Walls, 1942) and behavior (Schusterman, 1981; Levenson and Schusterman, 1997, 1999) supporting the idea that the pinniped eye possesses adaptations allowing function in water and under dark conditions.

The first photorefractive studies of pinnipeds showed that the eyes of these amphibious mammals were primarily suited for vision in water rather than in air (Johnson, 1893). Like most aquatic vertebrates, pinnipeds possess large, round lenses to compensate for the absence of corneal refraction under water (Walls, 1942). In air, where refraction occurs at both the round lens and the cornea, pinnipeds are myopic (Piggins, 1970). However, their stenopaic (slitlike) pupils functions as pinhole apertures to reduce the effects of myopia in air and provide relatively clear vision, at least as long as the pupil remains relatively small (Walls, 1942). Behavioral studies have confirmed the pupil's role in aerial acuity when it was demonstrated that visual acuity drops off much faster in air than under water as ambient light levels decrease (Schusterman and Balliet, 1971).

While the pupil's role in compensating for myopia in air is clear, the pupillomotor mechanism itself is controlled primarily by ambient light levels, irrespective of medium (Lavigne and Ronald, 1972). Like other mammals adapted for vision in dim conditions, pinnipeds possess large lenses and pupils, and densely packed, rod dominated retinas with well-developed choroidal tapeta (Walls, 1942; Landau and Dawson, 1970). The ability to dramatically alter pupil size is almost certainly an adaptation to regulate illumination of the light-sensitive retinas and functions only secondarily to improve visual resolution. Indeed, the pupillomotor response is probably essential to maintaining appropriate levels of photoreceptor stimulation during the rapid changes in light levels experienced by diving animals. In support of this conclusion, substantial differences in pupillary dynamic range between shallow and deep diving pinnipeds have been observed (Levenson and Schusterman, 1997). The deepest-diving pinniped, the northern elephant seal, was found to be capable of an over 400 fold increase in pupillary area, while shallow and moderately deep divers possessed considerably smaller ranges of only 25–200 fold (Levenson and Schusterman, 1997).

The functional significance of differences in pupillary structure can be seen clearly in a comparison of the dark adaptation rates of pinnipeds. Figure 3 depicts these rates for three species. In the inset of Fig. 3, the time necessary to reach maximum sensitivity is seen to be substantially faster for the elephant seal than for the shallower diving California

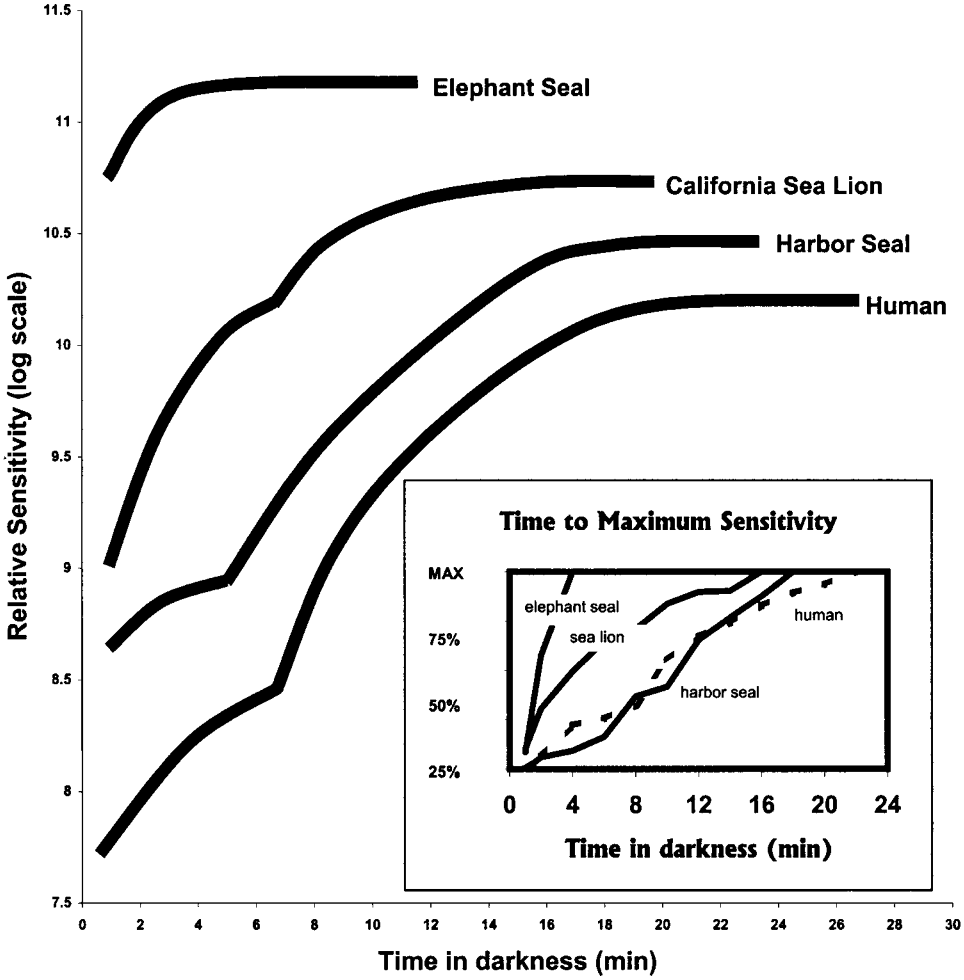

FIG. 3. Dark adaptation in three pinniped species and a human subject. Sensitivity values are reported on a relative log scale and were determined from the inverse of the each subject's white light threshold for each time interval. (Inset) Time to reach maximum sensitivity for three pinniped species and a human subject. Percentage values were calculated from sensitivity data as [(observed sensitivity/max sensitivity)*100]. Adapted from Levenson and Schusterman (1999).

sea lion and harbor seal. The 6-min dark adaptation time of the elephant seal (Levenson and Schusterman, 1999) matches the time it takes these seals to dive from the surface to foraging depths of 300–700 m (LeBoeuf and Laws, 1994), strongly implicating the visual sense in foraging ecology.

In addition to having rapid dark adaptation rates, elephant seals are highly light sensitive. This seal's extreme visual sensitivity directly relates to its ability to make long dives to great depths where ambient light levels are always low. Additionally, elephant seals possess specialized rod pigments that increase their sensitivity to the shorter wavelengths of light that predominate deep under water (Lythgoe and Dartnall, 1970). There are significant differences in maximum visual sensitivity between the elephant seal and shallow-diving species (Levenson and Schusterman, 1999), presumably because of the different conditions found in their respective foraging environments. Thus shallower diving harbor seals and California sea lions are less light sensitive than the elephant seal, and possess rod pigments that are only slightly short-wavelength shifted in sensitivity in comparison to those of terrestrial mammals (Lavigne and Ronald, 1975; Jacobs *et al.*, 1993).

These speculations about the importance of vision in foraging have recently been supplemented by observations of the Weddell seal, a deep diving phocid. Davis *et al.* (1999) obtained evidence that pinnipeds use backlighting to silhouette their prey while visually hunting. The researchers studied the hunting behavior of these seals beneath the Antarctic fast ice with a seal-borne video system. The seals were observed to stalk large Antarctic cod and smaller sub-ice fish whose silhouettes could be seen against the sunlight and ice above. During these observations of foraging in Weddell seals, these animals rarely vocalized, suggesting that echolocation was not the primary sensory system used for hunting fish prey beneath the ice.

Much remains to be learned about the visual capabilities of pinnipeds. However, the available evidence strongly suggests that their visual systems are primarily adapted for use under water. Pinnipeds have sacrificed the quality of their terrestrial vision in favor of enhancing their underwater capacities; natural selection in these animals has clearly favored the development of visual systems suited to foraging in an aquatic environment.

V. VIBRISSAE

Benthic-feeding dolphins have been observed to direct echolocation pulses into the substrate in order to detect prey (Rossbach and Herzing, 1997). These dolphins possess no apparent adaptation for benthic feeding, yet do so opportunistically using a biosonar system designed for use in the water. Pinnipeds that characteristically forage on the muddy sea floor tend to have modified vibrissae and facial structures used to detect and extract prey from the bottom (Reidman, 1990). The vibrissae of pinnipeds are apparently used to detect tactile and hydrodynamic stimuli very close to the source. The vibrissae of foraging Weddell seals were noted to become erect when they closed in on their fish prey (Davis *et al.*, 1999), suggesting that the vibrissae were used during the final stages of prey capture. Further, vibrissal function has been implicated in the short-range detection of ice holes by arctic phocids (see Reidman, 1990).

The extensive innervation of pinniped vibrissae, which can be up to ten times greater than that of terrestrial mammals (Hyvärinen and Katajisto, 1984), makes them well suited as a displacement detection mechanism (Dykes, 1975). Dehnhardt *et al.* (1998) experimentally demonstrated that a harbor seal was capable of detecting extremely weak hydrodynamic stimuli in the near field. These vibrations were several orders of magnitude below the particle velocities in the wake produced by a small swimming fish. Although probably useless for long range detection of prey or navigation, the vibrissae of pinnipeds likely function in close-range foraging and object detection when the visual sense is occluded or when prey is very close to the mouth and away from the line of sight.

VI. CONCLUSIONS

A highly sophisticated system of active biosonar has evolved only once in the marine environment, in a group of marine mammal predators—the odontocetes—that became completely tied to an aquatic existence early in their evolution. Echolocation in this group is linked to development of a high frequency signal production, reception, and signal processing system (Au, 1993). Because odontocetes were not evolutionarily constrained to give birth on land, the dolphin acoustic system became fully adapted for underwater functioning, allowing a refinement of the biosonar system not possible in amphibious mammals such as the pinnipeds. Because even the most aquatic pinnipeds must return to shore periodically and because airborne vocal communication appears to play an important role in most, if not all, pinniped social systems, selection pressures for highly sensitive, acute underwater hearing have not shaped the pinniped auditory system to as great an extent as they have in the dolphins.

All pinnipeds give birth on land or on ice, and terrestrial breeding activities have resulted in selection for retention of in-air hearing, primarily in the context of communication. Amphibious hearing ability has limited the sensitivity of hearing under water, where all pinnipeds must forage. Instead of developing a primarily sound-based system of underwater orientation, pinniped visual, tactile, hydrodynamic, and acoustic sensory systems were refined and incorporated into overlapping underwater perceptual channels that permit efficient underwater foraging and navigation without the use of active biosonar.

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[1] With pulse frequencies between about 10 and 100 kHz, the target strength of a 10-cm fish in side aspect would be between about −40 and −45 dB (Urick, 1983). A seal producing these pulses for the purpose of echolocation, at source levels of about 140 dB *re*: 1 μPa and having a detection threshold of about 65 dB *re*: 1 μPa should be able to detect such a fish in side aspect at a range of about 7.5 m. Similar calculations by Au (1990) for a bottlenose dolphin resulted in ranges of detectability for a fish of similar size of between 73 and 87 m. Given under-ice reverberation, ambient noise, the lack of a resonant swim bladder in Antarctic notothenioids, oblique target aspect, and relatively poor directional hearing in pinnipeds, the figure of 7.5 m is likely to overestimate the effective range of detection of a single fish by a Weddell or leopard seal.

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