

Pupillometry in seals and sea lions: ecological implications

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Abstract: Phocid and otariid pinnipeds forage almost exclusively under water, where observing them is difficult. As a result, little is known of how their senses are used while diving to locate and capture prey. In this study we used pupillometric methods to describe the relative visual abilities of three pinniped species: the northern elephant seal (*Mirounga angustirostris*), the harbor seal (*Phoca vitulina*), and the California sea lion (*Zalophus californianus*). The range of pupillary area and lower limit of pupillary adjustment were determined for each species. The northern elephant seal exhibited the largest range of pupillary area of the species examined. Furthermore, the elephant seal's pupil was found to reach maximum size only under extremely dim conditions. Both the harbor seal and California sea lion exhibited maximum pupillary dilation in conditions several log units brighter. These results indicate that the elephant seal's visual system is designed to function in dimmer conditions and to respond to greater changes in light levels than those of the harbor seal and sea lion. Such findings support the hypothesis that the visual systems of these pinnipeds are adapted for use in their respective foraging environments, and thus suggest that the visual sense is probably an important sensory modality used to locate and capture prey while diving.

Résumé : Les pinnipèdes phocidés et otariidés cherchent leur nourriture presque exclusivement sous l'eau où leur observation est difficile. L'intervention de leurs sens pour localiser et capturer leurs proies au cours des plongées est donc un phénomène mal connu. Au cours de cette étude, nous avons utilisé des méthodes pupillométriques pour décrire les capacités visuelles relatives de trois pinnipèdes, l'Éléphant de mer boréal (*Mirounga angustirostris*), le Phoque commun (*Phoca vitulina*) et l'Otarie de Californie (*Zalophus californianus*). L'étendue de la surface pupillaire et le seuil inférieur d'ajustement de la pupille ont été déterminés pour chaque espèce. Chez les trois espèces examinées, c'est l'Éléphant de mer qui possède l'étendue de surface pupillaire la plus large. De plus, la pupille de l'Éléphant de mer boréal atteint sa taille maximale seulement dans des conditions extrêmes de pénombre. Le Phoque commun et l'Otarie de Californie ont leur dilatation pupillaire maximale dans des conditions plus claires de plusieurs unités logarithmiques. Ces résultats indiquent que le système visuel de l'Éléphant de mer boréal est conçu pour fonctionner dans des conditions beaucoup plus sombres et peut s'adapter à des changements beaucoup plus importants d'éclairage que celui des deux autres espèces. Ces données supportent l'hypothèse selon laquelle le système visuel des pinnipèdes est adapté aux conditions du milieu où ils cherchent leur nourriture et il faut conclure que la vision est probablement l'une des modalités sensorielles le plus importantes dans la localisation et la capture des proies au cours de la plongée.
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Introduction

Pinnipeds are amphibious mammals, and belong to three families: Phocidae or "earless" seals, Otariidae or "eared" seals (which include fur seals and sea lions), and Odobenidae or walrus. While pinnipeds perform most reproductive activities on land or ice, they forage almost exclusively in water. As a result, relatively little is known about how they use their senses to locate and capture prey at sea. Most, if not all, pinnipeds produce sounds in air and under water, and many species are known to hear well under water (for reviews see Schusterman 1981; Richardson et al. 1995). However, the role of passive hearing during foraging has not

been documented in pinnipeds, and their ability to use echolocation (Poulter 1963, 1967; Renouf and Davis 1982) has been largely discounted (Evans and Haugen 1963; Schusterman 1967, 1968; Schevill 1968; Wartzok et al. 1984). The proximate nature of the tactile sense makes it ineffective for use in the long-range detection of free-swimming prey by pinnipeds, with the exception of the odobenids, who use their vibrissae to forage on sessile benthic invertebrates. While pinnipeds' eyes are similar to those of terrestrial mammals, there is evidence of good underwater visual functioning in species of both phocids and otariids (for reviews see Lavigne et al. 1977; Schusterman 1981).

The refractive index of water is different from that of air. As a consequence, most terrestrial mammals are hyperopic (far-sighted) in water. However, anatomical examinations of phocids indicate that at least some pinnipeds possess relatively acute vision under water as a result of adaptations of the cornea and lens (Piggins 1970; Wilson 1970). More importantly, behavioral studies of California sea lions (*Zalophus californianus*), a Stellar sea lion (*Eumatopias jubatus*), and a harbor seal (*Phoca vitulina*) indicate that these species possess visual acuity under water that is comparable to that

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of some primates in air; this is true for *Zalophus* spp. even under relatively low levels of illumination (Schusterman et al. 1965; Schusterman and Balliet 1970, 1971). Also, sea-water attenuates solar radiation, so ambient light levels are relatively low under water. As an adaptation for seeing in dim light, phocid and otariid pinnipeds possess large eyes (Pütter 1903, cited in Jameson and Fisher 1972), well-developed choroidal tapeta (Walls 1942), and densely populated, rod-dominated retinæ (Landau and Dawson 1970; Mass and Supin 1992), all of which increase light sensitivity. Furthermore, many species possess modified photopigments that specifically increase sensitivity to the types of light found beneath the ocean's surface (Lythgoe and Dartnall 1970; Lavigne and Ronald 1975). As these pinnipeds are well adapted to see under water, it has been proposed that they are heavily reliant upon their visual sense for detecting prey while diving to forage (Hobson 1966; Schusterman 1967, 1981).

Although available anatomical and behavioral data show that phocids and otariids are well-adapted to see under water and in dim light, there is little direct evidence that these animals are specifically adapted to use vision while diving, except one report on the "deep sea" rhodopsin of the deep-diving southern elephant seal (*Mirounga leonina*; Lythgoe and Dartnall 1970). If pinnipeds are able to use vision while diving to forage, they must be able to compensate for the large and rapid changes in ambient light levels experienced while diving from the ocean surface. It is largely for this reason that both phocids and otariids possess stenopaic pupils, which are slit-shaped in bright light and are capable of a great degree of dilation in darkness (Walls 1942). The small pupillary opening seen in bright light functions primarily to reduce excessive bleaching of the photopigments (Barlow 1972; Lavigne and Ronald 1972). Theoretically, the slit-shaped pupil of pinnipeds also provides a large range of pupillary area (Lavigne and Ronald 1972; Wilcox and Barlow 1975) and may increase an animal's ability to detect visual stimuli during the first minutes of darkness (Woodhouse and Campbell 1975). The problem, however, is that phocids and otariids forage in a variety of environments and experience different changes in light levels while diving and different ambient conditions while foraging at depth. If these pinnipeds have evolved to be able to locate prey visually under water, then each species must exhibit visual abilities, such as those imparted by pupillary function, that reflect the conditions it typically experiences while diving to forage. Indeed, this adaptation would be beneficial not only for prey detection but for a variety of underwater orientation tasks, such as avoidance of predators.

For instance, northern elephant seals (*Mirounga angustirostris*) dive to depths of 500 m or greater (Le Boeuf et al. 1988), while harbor seals and California sea lions rarely dive to depths of over 100 m (Feldkamp et al. 1989; Boness et al. 1994). Assuming that these pinnipeds use vision while diving to locate and capture prey, the elephant seal's visual system should be capable of functioning in more light-limited conditions and compensating for larger changes in light levels than the visual systems of the harbor seal or California sea lion.

The observation of pupillary structure and function is known as pupillometry. Pupillometric techniques can be used comparatively to describe the type of lighting conditions in

which an animal's visual system is adapted to function (DeGroot and Gebhard 1952; Wilcox and Barlow 1975; Hughes 1977). To demonstrate that phocids and otariids possess visual abilities that are adapted for use in their respective underwater foraging environments, pupillometry was performed with three species: the northern elephant seal, harbor seal, and California sea lion. Because the northern elephant seal experiences the largest changes in light levels while diving and the dimmest conditions while foraging at depth of the three species, we hypothesized that it would possess the lowest lower limit to the range of pupillary adjustment and the largest range of pupillary area. The lower limit of pupillary adjustment is the light level at which pupillary constriction ceases. The harbor seal and California sea lion dive to forage at similar depths in relatively similar environments, so we predicted that these species would exhibit similar pupillometric responses.

Methods

Subjects

Data were collected from May to December 1995. The subjects for the experiment were Burnyce, a 2½-year-old, 197-kg northern elephant seal, Sprouts, a 7-year-old, 79-kg harbor seal, and Rio, a 9-year-old, 68-kg California sea lion. The animals were housed in salt-water pools at Long Marine Laboratory, Santa Cruz, California. Operant-conditioning techniques, using only positive reinforcement, were used to train the animals for the experiments. Animals were cared for in accordance with the principles and guidelines of the Canadian Council on Animal Care (1993).

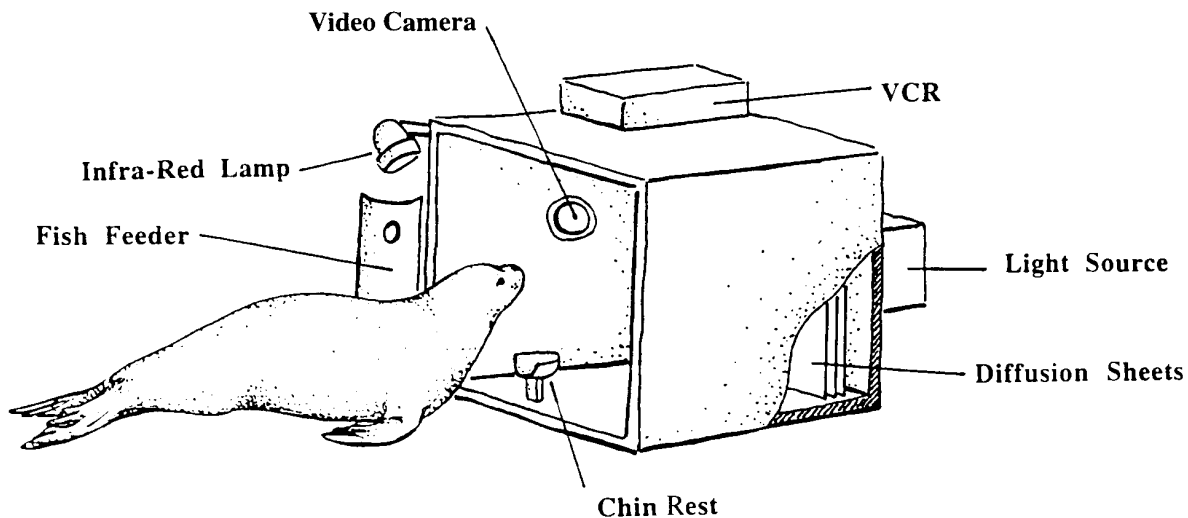
Materials

All experiments were conducted in a lightproof room, using the apparatus depicted in Fig. 1. The light source for the pupillometric apparatus consisted of four 25-W white fluorescent lamps and was attached to the back of a large, open-ended white box. A PVC chin rest located just inside the front end of the cube was used to fix the animal in position for each session. As the cutaway portion of Fig. 1 shows, three white cloth diffusion sheets were permanently fixed between the light source and the animal to reduce the directional component of the light. Light levels were attenuated during experiments by placing neutral-density filters between the light source and the diffusion sheets or by extinguishing the light source. Visible ambient light levels were measured at the chin rest with a Goldilux® foot-candle meter (response accuracy $\pm 3\%$). Since the pupillomotor response of pinnipeds to ambient light has been found to be the same in air and under water (Lavigne and Ronald 1972), the results obtained are indicative of pupillary function in either medium.

The brightest light condition occurred when no filters were placed in front of the light source. This light level, used for light adaptation averaged 88.5 ± 6.5 foot candles (1 foot candle = 10.764 lx), which is equivalent to normal indoor lighting. The next brightest light level averaged 3.4 ± 0.6 foot candles, and occurred when one 10%-transmission neutral-density filter was used. The average light level with two and three filters was 0.3 ± 0.07 and $0.03 \pm 6 \times 10^{-3}$ foot candles, respectively. All other experimental light levels used fell below the sensitivity of the light meter. Therefore, for each additional 10%-transmission filter used, light levels were considered to have decreased by one additional log unit. When the light source was extinguished, ambient conditions were referred to as "total darkness."

The pupillary response was recorded using an infrared-sensitive video camera aimed at the animal's left eye through a hole in the pupillometric apparatus (see Fig. 1). An infrared lamp, fitted with

Fig. 1. Subject preparing to station in the chin rest at the base of the pupillometric apparatus so that its pupillary response can be filmed.



a visible-light-blocking filter, was used to increase infrared light levels for filming during experiments. Pinnipeds are insensitive to infrared light (Lavigne and Ronald 1972) and none of the animals exhibited any pupillary response to the infrared light when it was turned on and off in close proximity to the eye. Therefore, it was not considered to have affected the amount of visual stimulation. Video output was recorded with a VHS-type videocassette recorder (VCR).

Procedure

For experimental sessions the animals were moved to the test area from an adjacent pool and trained to remain stationary with their head on the chin rest for 8–10 min. The only movements during an experimental session occurred when the animal briefly lifted its head to take a food reward from the "fish feeder," a small hole in the side of the pupillometric apparatus (see Fig. 1). Feeding typically occurred 15–20 times per session.

To insure consistent visual-adaptation conditions, each animal was light-adapted in bright light for the first 3 min of each experimental session. Minimum pupil size was measured during the final minute of this period. After 3 min, the light source was attenuated using neutral-density filters. Each session continued for 5 min after the filters were added, though less than 3 min were typically required for the pupillary area to become stable. The light level was measured at the chin rest before and after attenuation. In some sessions the light source was extinguished after the 3-min light-adaptation period to create total darkness in order to obtain images of maximum pupillary dilation for each animal.

Pupil size was determined using digitized video images created from the video recordings. To eliminate image distortion, as well as to insure that the pupil was stable and had adequate time to dilate, images to be digitized were selected according to the following criteria: the animal had to be looking towards the camera, the animal had to remain motionless in the chin rest for at least 5 s prior to image selection, and, in darkened conditions, at least 3 min must have passed since attenuation. Video images were calibrated with the digitized image of a metric ruler filmed at the end of each session. The calibrated images were then used to determine apparent pupil areas in square millimetres.

The percentage of maximum size was calculated by dividing the pupillary area observed for each animal at each light level by the animal's maximum pupillary area. The lower limit of pupillary adjustment was defined as the light level at which the pupil dilated

to over 90% of maximum size. Upper limits were not determined, as we were unable to expose the animals to sufficiently bright conditions. Experimental sessions were performed at progressively lower light levels until the lower limit of pupillary adjustment was determined for each animal. With our limited range of neutral-density filters we were unable to achieve 90% or greater dilation in the elephant seal. However, there was a large difference in pupillary area for this animal between the lowest light level tested ($\sim 3 \times 10^{-9}$ foot candles) and total darkness, indicating that the pupil had adequate time to dilate and that a substantial degree of constriction was occurring at this light level. The range of pupillary area was calculated by dividing each animal's average maximum pupillary area by its average minimum pupillary area.

Results

Pupillometry was performed at 7 light levels for the harbor seal and California sea lion and 12 light levels for the northern elephant seal. Pupillary areas and percentages of maximum pupillary size are presented in Table 1 for each species at each light level tested. As indicated, the northern elephant seal possessed the smallest pupil in bright light and the largest pupil in total darkness. The northern elephant seal was also found to possess a lower percentage of pupillary dilation than either the harbor seal or the sea lion at all non-zero light levels tested.

Actual video images of the pupils of all three species in relatively bright light (~ 85 foot candles), very dim light ($\sim 3 \times 10^{-4}$ foot candles), and total darkness are presented in Fig. 2. As the top row of this figure illustrates, the constricted pupils of all the animals examined were vertical slits in bright light. Note that the pupil of the elephant seal is much smaller than those of the other species at this light level. The middle row of Fig. 2 illustrates the large difference in percentage of dilation seen between the species at many of the light levels tested. Images of the fully dilated pupils of all three species are presented in the bottom row of Fig. 2. Maximum pupillary size for the elephant seal was almost twice that for the California sea lion and over 2½ times that for the harbor seal.

Percentages of maximum size for all three species at all

Table 1. Pupillary areas and percentages of maximum size for three pinniped species.

Illuminance level (foot candles)	Northern elephant seal		Harbor seal		California sea lion	
	Pupillary area (mm ²) ^a	%	Pupillary area (mm ²) ^a	%	Pupillary area (mm ²) ^a	%
~85	0.9±0.3	0.2	2.3±0.6	1.4	8.4±1.5	3.8
~3 × 10 ⁰	6.5±2.6	1.5	18.1±7.3	11.1	108.8±9.3	49.5
~3 × 10 ⁻¹	10.0±3.3	2.4	72.2±21.3	44.6	166.8±15.1	75.8
~3 × 10 ⁻²	23.3±8.9	5.5	112.6±13.3	69.5	180.3±12.1	82.0
~3 × 10 ⁻³	37.7±19.9	8.9	139.7±8.5	86.3	193.7±16.6	88.1
~3 × 10 ⁻⁴	93.3±22.6	22.1	150.9±7.0	93.1	204.8±20.3	93.1
~3 × 10 ⁻⁵	142.2±14.7	33.7				
~3 × 10 ⁻⁶	255.2±78.9	60.4				
~3 × 10 ⁻⁷	266.9±39.4	63.2				
~3 × 10 ⁻⁸	254.6±41.9	60.3				
~3 × 10 ⁻⁹	331.2±37.3	78.4				
Total darkness	422.3±9.8	100.0	162.2±10.2	100.0	219.9±9.5	100.0

^aValues are given as the mean ± standard deviation.

Table 2. Ranges of pupillary area for five pinniped species and the domestic cat.

	Pupillary area			Reference
	Max. (mm ²)	Min. (mm ²)	Range (max./min.)	
Northern elephant seal	422.3	0.9	469.2	
Harbor seal	162.2	2.3	70.5	
California sea lion	219.9	8.4	26.2	
Harp seal	208.4	1.94	107.4	Lavigne 1973
Ringed seal	123.65	0.485	255.0	Lavigne 1973
Domestic cat	123	0.9	136.7	Wilcox and Barlow 1975

light levels tested are compared in Fig. 3. The lower limit of adjustment for both the harbor seal and the sea lion was found to be at $\sim 3 \times 10^{-4}$ foot candles. At this light level the elephant seal's pupil had achieved only 22.1% of maximum size (see Fig. 2). The lower limit for the elephant seal occurred between $\sim 3 \times 10^{-9}$ foot candles and total darkness. As Fig. 3 illustrates, the elephant seal exhibited maximum dilation at light levels that were several log units dimmer than those required for maximum dilation in the harbor seal or sea lion.

Ranges of pupillary area for the three pinniped species examined here, as well as the harp seal (*Phoca groenlandica*), the ringed seal (*Phoca hispida*), and the domestic cat (*Felis domesticus*), are presented in Table 2. Pupillary ranges for the harp seal and ringed seal are taken from Lavigne (1973) and the data for the cat from Wilcox and Barlow (1975). The range of pupillary dilation for the elephant seal was much higher than that of any of the other pinniped species examined, more than 18 times that of the California sea lion. The range of pupillary area for the harbor seal examined here was the lowest for the phocids, though it was relatively close to that of the harp seal. Lavigne (1973) reported that the pupillary range for the harbor seal was 71.38. Since this is similar to our finding, it is not shown in Table 2. The California sea lion had a much smaller range

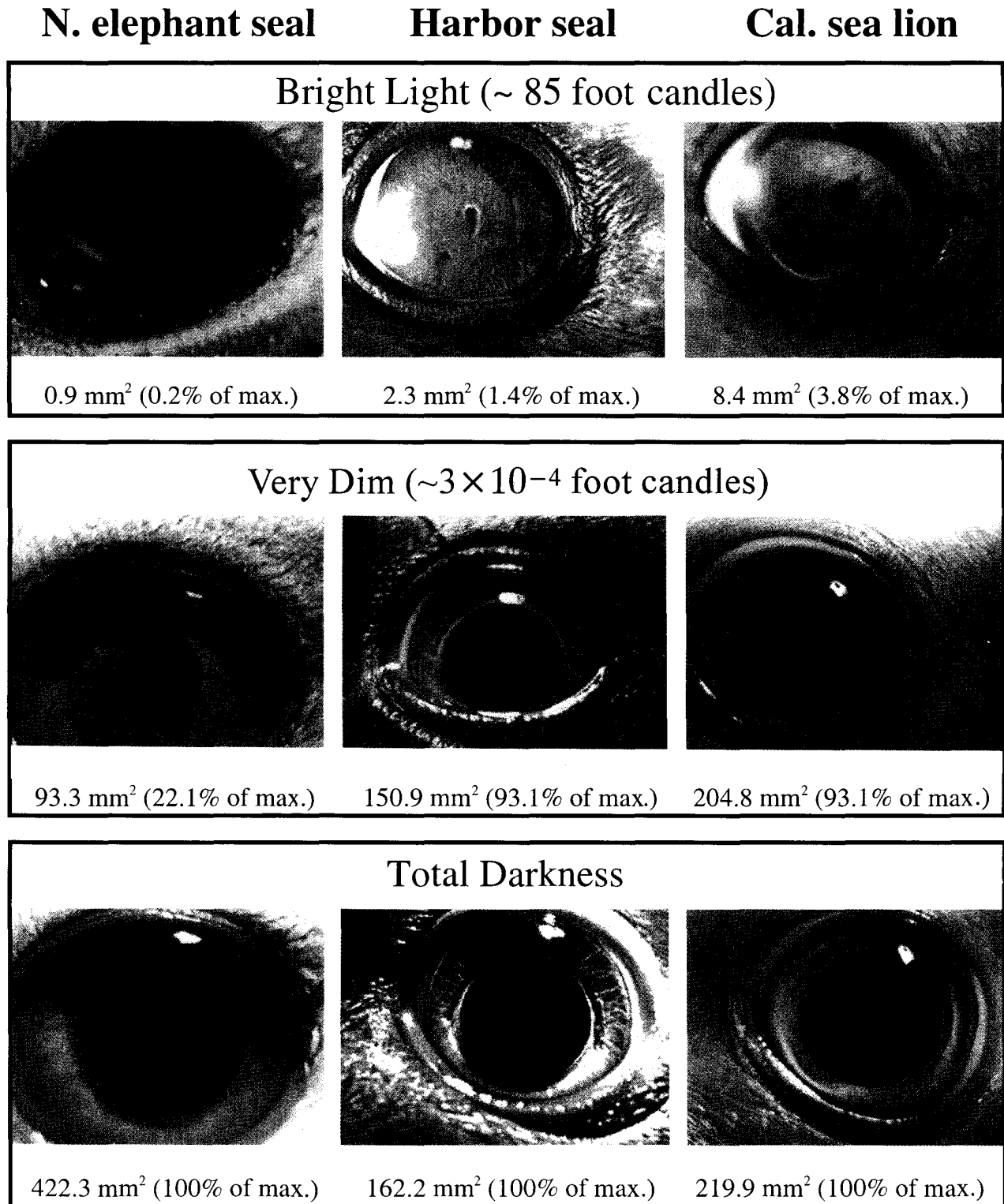
than the other pinnipeds. Its range was less than half that of the harbor seal, which had the next smallest value. All the pinnipeds except the elephant seal and ringed seal had ranges that were less than or equal to that of the cat.

Discussion

Pinnipeds, like most mammals, possess rod photoreceptors that are similar in structure to those of humans (Landau and Dawson 1970; Nagy and Ronald 1972). It is known that under ideal conditions, human rods are sensitive to as little as one photon of light (Hecht et al. 1942). It is likely, then, that under ideal conditions, pinnipeds possess the same remarkable light-sensing ability. However, the conditions found in nature are rarely ideal. For this reason, the results obtained here do not reflect differences in the absolute visual sensitivities of these animals per se, but differences in the ranges and limits of light levels over which their visual systems have evolved to operate. Although the sample size was limited, it is clear from these results that differences in visual ability, as indicated by pupillary structure and function, do exist between the pinniped species examined here.

As pupillary function is integral to visual function for mammals, the analysis of pupillary structure and behavior can be used to describe the lighting conditions for which a

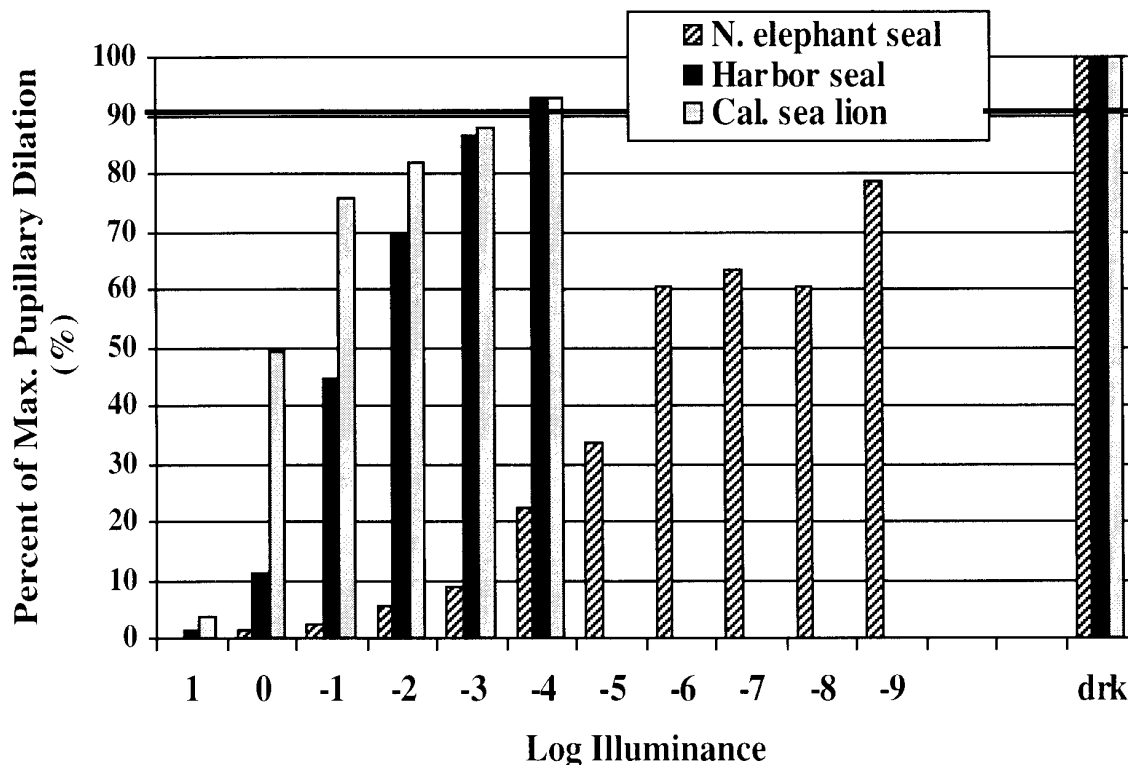
Fig. 2. Actual images of the pupils of the northern elephant seal, harbor seal, and California sea lion in bright light, very dim light, and total darkness. Note that the images do not have the same scale. The pupillary area and percentage of maximum pupillary dilation are shown below each image.



species' visual system is designed, particularly when comparing closely related species. However, because factors other than retinal illuminance, such as state of arousal or

state of adaptation, may also affect the pupillomotor response, the exact nature of pupillary behavior often varies among taxonomic groups (see Walls 1942). For this reason, as well

Fig. 3. Percentage of maximum pupillary size versus log illuminance (foot candles) for the northern elephant seal, harbor seal, and California sea lion; "drk" indicates total darkness.



as the differences in experimental design and light measurement from Lavigne (1973), lower limits of adjustment were only compared between the three pinniped species examined here.

Pupillary constriction in the elephant seal at $\sim 3 \times 10^{-9}$ foot candles demonstrates that its visual system is operating to regulate light capture in these conditions. This shows that the elephant seal's visual system is adapted to function in very dim environments. Furthermore, the elephant seal's lower limit of adjustment was considerably lower than that for either the harbor seal or sea lion; neither of these shallower diving species showed pupillary constriction below $\sim 3 \times 10^{-4}$ foot candles. Assuming that the visual systems of these species are relatively similar in anatomy, the lower limit of adjustment exhibited by the elephant seal shows that its visual system is adapted to function in dimmer ambient light conditions than those of the other species. Likewise, the fact that the harbor seal and California sea lion possess the same lower limit of adjustment shows that their visual systems are adapted for use in similar environments. Both these conclusions are consistent with the known diving and foraging behaviors of these species.

Since the harbor seal and sea lion rarely dive for more than 10 min (Feldkamp et al. 1989; Boness et al. 1994), and the elephant seal typically reaches maximum depth in about 5 min (Le Boeuf et al. 1992), there is little time for retinal adaptation. Thus, pupillary function must be of considerable importance to these animals, as it is the only adaptive mechanism rapid enough to be effective over this time scale. As retinal illumination varies directly with pupillary area, the range of pupillary area represents the maximum change in

light levels to which the pupillary response is effective. In view of this, it was not surprising to find that the ranges of pupillary area obtained here showed a clear relationship between diving/foraging behavior and visual ability in these species.

A pinniped diving to 100 m experiences a change in ambient illumination of at least two log units in intensity (estimated for 490 nm in pure water; Lythgoe 1979). For an animal diving to 500 m, ambient light levels decrease by at least an additional four log units. Thus, it is not surprising that the elephant seal had a much larger range of pupillary area than the other, shallower diving pinnipeds; it must adapt to larger changes in light levels in the same short period of time. The small ranges of the harbor seal and California sea lion are indicative of the small changes in light levels experienced by these species while diving. Although the harp seal and ringed seal are not considered deep divers (Lydersen and Kovacs 1993; Kelly and Wartzok 1996), they were found to possess ranges that were higher than those of the harbor seal and sea lion. While other ecological factors may be involved, the increased pupillary ranges of the harp seal and ringed seal are probably the result of the extremely bright and reflective surface conditions of the polar environment that they inhabit.

While the light levels used to obtain pupillary ranges are not always consistent between studies, the nearly identical results obtained here and by Lavigne (1973) for the harbor seal suggest that a similar range of light levels was used, and support the comparisons made between the two studies. However, Wilcox and Barlow (1975) determined the range for the cat, using a wider range of light intensity than that used for the pinnipeds. Although the range for the cat is an overestimate when compared with those of the pinnipeds, the

results reported in Table 2 still agree with Hughes' (1977) predictions, based on other ocular dimensions, that cats are adapted to function over a wider range of light levels than pinnipeds. Only the elephant seal and ringed seal possessed larger ranges, and both these species exhibit specialized foraging behaviors: one is an extremely deep diver and the other forages exclusively in polar environs.

As the harbor seal and California sea lion dive to forage in similar environments, possess similar visual acuity, and were found to possess similar lower limits of adjustment, we predicted that they would possess similar pupillary ranges. Therefore, we were surprised to find that instead, they had substantially different ranges of pupillary area. One possible explanation is that, compared with the harbor seal, the California sea lion perhaps forages in less light-limited environments, i.e., in shallower water, or forages more strictly at night. Either behavior would reduce the magnitude of the changes in light levels experienced by the sea lion and would reduce the need for a large pupillary range. It is also likely, however, that the California sea lion eye relies upon other mechanisms of adaptation, such as pronounced cone function and retinal adaptation to maintain sensitivity while diving. The development of cone function would also serve to increase visual acuity in bright conditions, which may be of increased importance to the California sea lion during social interactions both in air and under water.

In general, the results of the current study support the hypothesis that many pinnipeds use vision to detect prey while diving to forage. The trends seen in pupillary structure and behavior suggest that phocids and otariids possess visual systems that are adapted to the conditions in their respective underwater environments. Comparisons of our two pupillometric measures, i.e., the limit of adjustment and pupillary range, indeed showed a strong correlation between diving behavior and visual ability in these phocid and otariid pinnipeds. The harbor seal and California sea lion, species that forage in similar environments, were found to possess relatively similar pupillary mechanisms. In contrast, the deep-diving elephant seal was found to possess the lowest lower limit of pupillary adjustment and the largest range of pupillary area of the pinnipeds examined.

Acknowledgments

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