Cornell University
Shoals Marine Laboratory
BioSM 3210: Anatomy and Function of Marine Vertebrates
Dr. Frank Fish

The Doe-Eyed Effect: It's Not Just an Optical Illusion
Eye Orbit Size Relationship to Dive Depths in Pinnipeds

Caitlin Etri

August 4, 2013

Introduction

By land or by sea, all organisms on Earth are phylogenetically related to one another. Take a look at deer for example—their increased agility, camouflaged coats, and large eyes are examples of adaptations that have evolved to increase the chances of survival among species. Some adaptations are similar across clades, for example, the ichthyosaur and the owl. Both are known for having incredibly large eyes. The ichthyosaur expressed this adaptation dating back as far as 250 million years ago. So why are large eyes still seen today? Large eyes can serve different purposes depending on the habitat of the organism, primarily to enhance vision.

The ichthyosaur is a prehistoric marine reptile whose visual acuity was enhanced by its abnormally large eyes (Humphries & Ruxton, 2001). Ichthyosaurs had to be adapted to diving in waters as deep as 500 meters, which might explain why their large eye diameter is an adaptative feature to increase the resolution of an image in low-light areas (Humphries & Ruxton, 2001). Organisms have evolved for combating the vision differences among air and water environments (Hanke et. Al, 2009). For marine mammals, large eyes are crucial for obtaining food deep within the water column where light is limited.

In this experiment we examined eye orbit size to dive depths (both foraging and deep) in Pinnipeds. We questioned whether or not having large eyes was an evolutionary advantage that correlated with how deep a particular species can dive. As depth increases, availability of ambient light decreases dramatically, thereby negatively affecting one's vision. A recent study was performed investigating osteological correlations between deep diving Pinnipeds. Their results support our conclusion that large eyes are beneficial for marine mammals that enter low-light oceanic zones. A larger eye holds more photoreceptor cells, which increase the amount of light coming in through the cornea, subsequently enhancing vision (Debey & Pyenson, 2013).

Diet is indirectly related to eye orbit size. The specimen used for the gray seal expressed the largest eye orbit diameter to skull ratio, in addition to the highest foraging and deepest dive depths. Since gray seals most commonly perform benthic dives in low-light areas to obtain their prey , we hypothesized they will need to have the largest eyes out of our sample set (Jessopp et al., 2013).

Materials and Methods

Five species in the Pinnipedia were compared against one another in search of a correlation between eye orbit diameter and diving depths. This was executed by performing a series of measurements on the cranial skeletons of five species in Pinnipedia*.* The sample size was limited by the availability of skulls in the Pinniped clade. Some species are represented twice due to the availability of multiple cranial skeletons. This applies to the California sea lions and harbor seals. The sample set of the experiment included the following (sample size of each family, common name and scientific name, respectively): (1) Crabeater Seal (*Lobodon carcinophagus)*, (1) Gray seal (*Halichoerus grypus)*, (2) Harbor Seals (*Phoca vitulina),* (2) California Sea Lions (*Zalophus californianus),* and (1) Walrus (*Odobenus rosmarus).* The majority of the samples were skull replicates from the California Academy of Science, with the exception of one harbor seal (*Phoca vitulina)* and the walrus (*Odobenus rosmarus),* which were skull specimens from deceased Pinnipeds supplied by Shoals Marine Laboratory. Three families from the Pinniped order were represented within the sample set: Phocidae (Crabeater, Gray, and Harbor Seals), Otariidae (California Sea Lion), and Odobenidae (Walrus). The three families reduced sample bias, allowing us to look at the variances that can occur within the Pinniped clade.

Four measurements were recorded to obtain the average total eye diameter. As shown in Figure 1, the diameter of the eye was measured latitudinally and longitudinally (yellow and red arrows, respectively) using a caliper. The yellow arrow measured across from the two processes in the eye orbit, while the red measured longitudinally from the supraorbital to infraorbital of the eye orbit. The latitudinal measurements among individual skulls served as a better proxy for the eye orbit diameter since there were two processes that existed in each skull. The longitudinal length was not accurately standardized. It allowed for variation because it was not a direct measurement between two processes, and instead, more of a topographic point. There was potential for measurement points to differ among individuals. To compensate for the non-homologous measurements, it was necessary to average all morphological data together to increase accuracy in determining true eye orbit sizes. This was done for both the left and right eyes, and both were averaged together to get a total average eye diameter using all four measurements for each individual. All measurements were imported to Excel 12.2.0 where the calculations were performed. Data tables were imported into JMP 10.0 to provide statistical results. To correct for differences in size among species, a ratio was taken between total average eye diameter and skull length of each individual. The skull length values

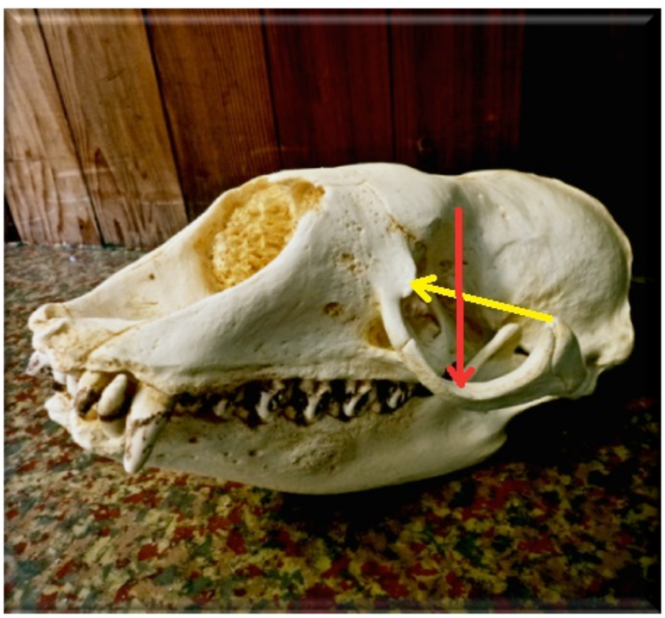

Figure 1: Cranial skeleton of a Crabeater seal (*Lobodon carcinophagus)* representing direction and placement of caliper for eye orbital measurements. Yellow: latitudinal, Red: longitudinal.

were measured from the tip of the rostrum to the processes behind the skull. Foraging and deepest dive depth values of each investigated species were used from recent literature.

Results

In Figure 2, the average total eye diameter (left, right, latitudinal, and longitudinal averaged measurements) is graphed against the skull length (mm). As skull length increased, eye diameter did as well. Data tables were imported into JMP 10.0 to provide statistical results. A significant R^2 value of 0.91 is expressed with $p < 0.009$ (Figure 2).

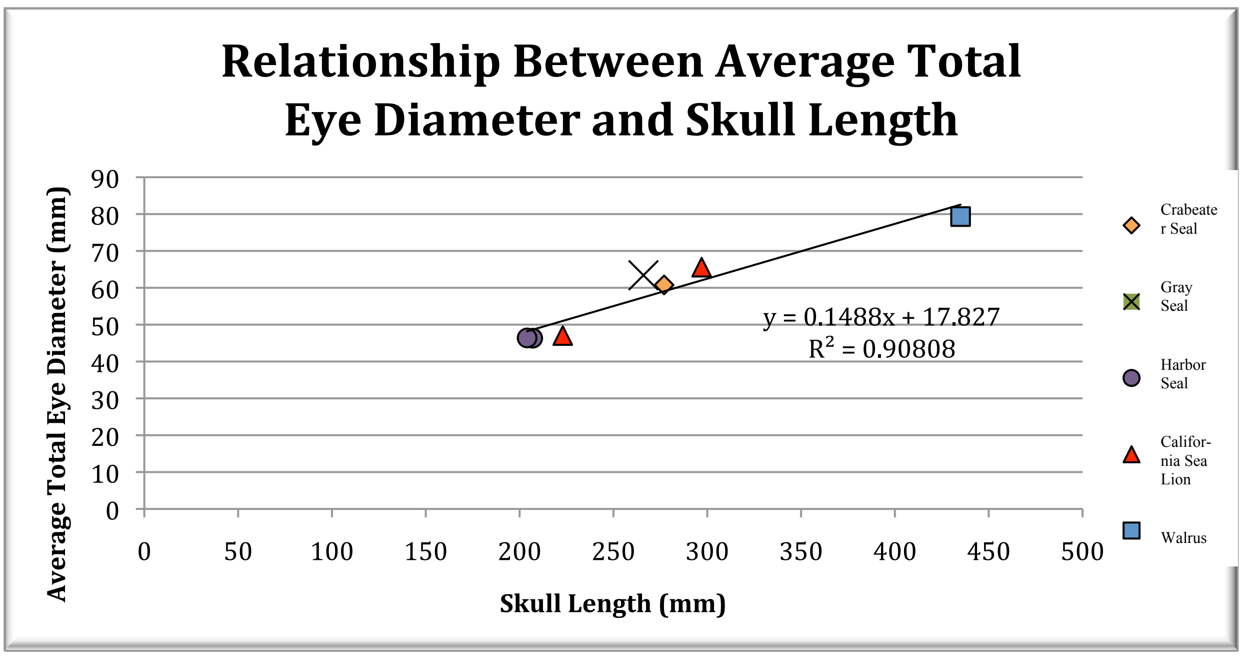

Figure 2: A regression line compares the relationship between the average total eye diameter (mm) (including both longitudinal and latitudinal measurements) to skull length (mm). R^2 =0.91 and p value < 0.0009 ($p < .05$).

Figure 3 illustrates the relationship between foraging dive depths and the arcsin of total averaged eye diameter ratio. The arcsin of the eye diameter to skull length ratio was taken for both Figures 3 and 4. Increasing foraging dive depth (m) shows a significant increase in the total eye diameter ratio. Regression lines state an R^2 value of 0.70 and $p < .02$ (Figure 3).

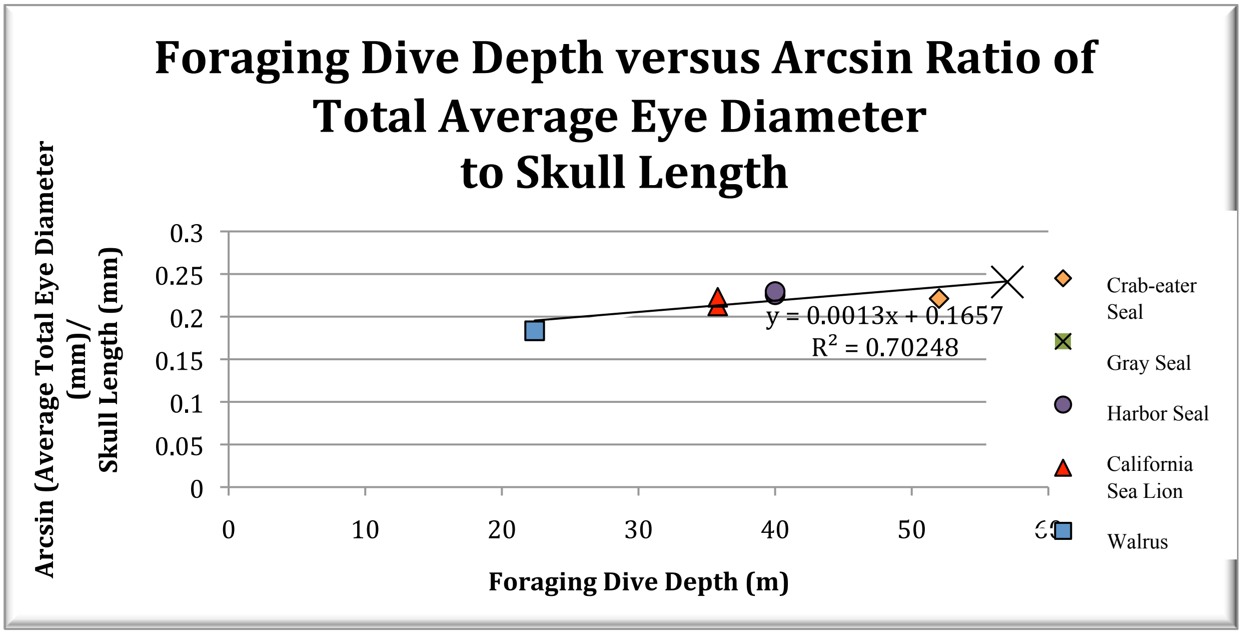

Figure 3: A regression line comparing foraging dive depths (m) to Arcsin of the ratio between average total eye diameter (mm) and skull length of the five selected species. $R^2 = 0.70$ and $p < 0.02$ ($p < .05$).

The gray seal (*Halichoerus grypus)* had the deepest foraging dive depth of 57 m, while the walrus (*Odobenus rosmarus)* expressed the shallowest foraging dive depth of 22.4 m (Table 1). In both Figures 2 and 3, the order of increasing foraging and deepest dive depths of each species was: Walrus (*Odobenus rosmarus),* California sea lion (*Zalophus californianus),* Harbor seal (*Phoca vitulina)*, Crabeater seal (*Lobodon carcinophagus)*, and finally the gray seal (*Halichoerus grypus)*. Deepest dive depths range from 67 meters, Walrus (*Odobenus osmarus),* to 528 meters, gray seal (*Halichoerus grypus)* (Table 1).

Species Common Name	**Species Scientific Name**	**Foraging Dive Depth (meters)**	**Author, Year**	**Deepest Dive Depth (meters)**	**Author, Year**
Walrus	*Odobenus osmarus*	22.4	Gjertz et al, 2000	67	Gjertz et al, 2000
California Sea Lion	*Zalophus californianus*	35.8	Weise et al, 2010	306	McDonald & Ponganis,

					2012
Harbor Seal	*Phoca vitulina*	40	Bajzak et al, 2012	418	Eguchi & Harvey, 2005
Crabeater Seal	*Lobodon carcinophagus*	52	Nordoy & Folkow, 1995	455	Nordoy & Folkow, 1995
Gray Seal	*Halichoerus grypus*	57	Jessopp et al, 2013	528	Jessopp et al, 2013

Table 1: Compiled data set of deepest and foraging dive depths recorded in recent literature.

As deepest dive depths increase, the arcsin of the ratio of eye orbit diameters to skull length also increases (Figure 4). A regression line for this relationship provides a significant R^2 value of 0.90 and $p < .0015$ (Figure 4).

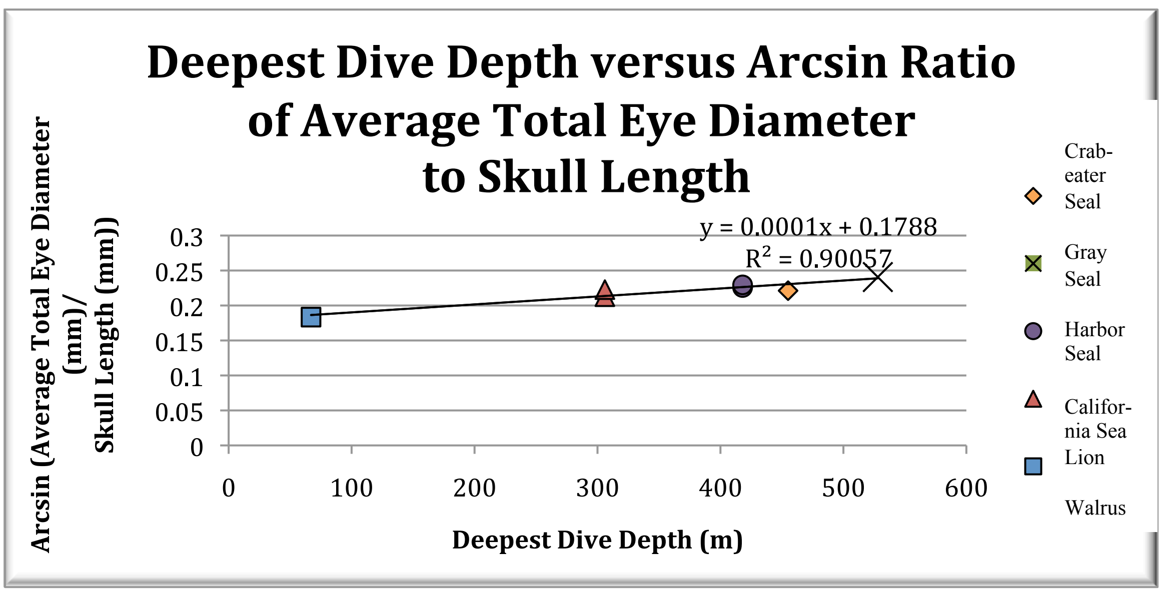

Figure 4: Deepest dive depths (recorded in recent literature) were compared to the arcsin of average total eye diameter (mm) to skull length (mm). A regression line provides the statistical results of an R^2 value of 0.90 and a p value of 0.0015 ($p < .05$).

Discussion

The gathered results show a positive correlation between eye orbit size and diving depths (both foraging and deep diving) in Pinnipedia. This supports the hypothesis that large eyes become increasingly necessary and are evolutionarily adapted for low light levels that are experienced deeper within the water column. Large eyes were also observed to increase with skull size (Figure 2). Our findings supported the results from Debey & Pyvenson (2013) which also determined a direct relationship between eye orbit size and skull length. The eye diameter is a proxy for the actual eyeball size that existed in the living mammal. The results were significant for both foraging and deep dives in relationship to average total eye diameter among the species (Figures 2 & 3) with p values of less than 0.02 and 0.0015, respectively. Aquatic mammals need to be adjusted to living and surviving in low-ambient light conditions, especially on deeper dives in the benthic zone. As a result, there are special adaptations that these animals have, Pinnipeds specifically, that help them prosper in diminished light. The foundation for their success and survival starts with large eyes.

The composition of an eye that is acclimated for both mediums of air and water requires certain features to overcome difficulties associated with low-light areas that impact their diving depths. Aquatic mammals are emmetropic in both air and water. Emmetropia refracts the light to focus on the retina to give them perfect vision (Mass & Supin 2007, Hanke et al. 2009). Aquatic mammals have a very thick, developed tapetum lucidum. This reflective layer gives them better vision in the low-light waters by increasing stimulation of photorecepter cells (Ollivier et al, 2004). A high density of ganglion cells in the eye has also been determined to increase visual acuity (Hanke et al., 2009). The performed density experiments by Mass et al. (2007), show a correlation with high density areas of ganglion cells to high visual resolution. In addition, large pupils act similarly to enhance underwater vision. Large pupils allow more surface area to let light in to heighten visual sensitivity (Levenson & Schusterman, 1999). All of these factors combined enable Pinnipeds to be evolutionarily successful in (and out of) the water. Subsequently, in this experiment, eye diameter size showed a positive relationship with increased diving depths (decreased light availability). The correlation between eye orbit size and pupil diameter support the findings of Debey and Pyvenson (2013). "*In living vertebrates, visual sensitivity is a function of both photoreceptive cell number as well as eye diameter: larger eyes can house more retinal photoreceptive cells, and the absolute size limits incoming light* (Debey & Pyvenson, 2013)."

Subsequently, large eyes (large pupils) are evolutionary adaptations for adjusting to low-light benthic zones within the water column. The trends in our experiment show a correlation between large eye diameter and deeper diving depths. Larger eyes are better equipped for deeper diving depths since increasing pupil size allows more light to be received. The gray seal (*Halichoerus grypus)* had the largest eye diameter of all in addition to the both the highest foraging and deepest dive depths. Gray seals are generalists that perform the majority of their dives in the benthic region (57 meters, Table 1) (Jessopp et al., 2013). This would imply that they would need large eyes to hunt for prey in the dark benthic habitats. This assumption is validated by our results (Figures 3 and 4), which show that gray seals have the largest average eye orbit diameter ratios compared to the other species in our sample set. On the other end of the spectrum, walruses (*Odobenus osmarus)* exhibit the smallest eye diameter to skull length ratio, implying that they have the smallest eyes, and therefore do not forage in deep waters. Small eyes are not ideal for deep divers since their pupil surface area (and decreased number of photoreceptor cells) would not be enough to allow enough light in to see properly (Hanke et al., 2009). Fortunately, their prey (mollusks) is located in shallow pelagic zones (Gjertz et al., 2000). Figures 3 and 4 represent the small eye diameter of the walrus compared to its shallow diving depths. In the middle of the group (of increasing eye diameter to dive depths) are California sea lions, harbor seals and crabeater seals. California sea lions (*Zalophus californianus)* are generalists that feed in waters less than 50 meters deep on mainly schooling fish such as anchovies and sardines (Weise et al., 2010). Harbor seals feed in the intermediate levels between the pelagic and benthic zones, due to the location of their prey (benthic fishes and mollusks). They are opportunistic predators—how deep they dive for food relates to where in the water column their prey are (Eguchi & Harvey, 2005). Crabeater seals' foraging depths varied seasonally. During the summer months when upwellings occur, crabeater seals are recorded to have deeper foraging depths due to the increased productivity of plankton (Nordoy & Folkow, 1995). Their large eye orbit sizes are adapted for shallow and deep dives of varying light ambiance.

Marine mammals are well adapted to survive and flourish in some of the darkest places on Earth. Their heightened visual sensitivity, thickened tapetum lucidum, high density ganglion cells and large pupil size allow them to see like an owl in the dark. Our conducted research results support previous conclusions by Debey and Pyenson (2013) regarding eye orbit size to diving depths. There was a high significance between increased average total eye orbit size in our investigated Pinniped species, to increased foraging and deep diving depths. Larger eyes support larger pupils, which are able to collect more light in low-light areas such as the benthic regions (thereby enhancing vision). Using the dive depth values from recent literature, we applied the diets of Pinnipeds to the prey's location in the water column. The diet of gray seals (*Halichoerus grypus)*, consists mainly of benthic fishes. This would imply the need for larger eye diameters that correlate with increased diving depths in the water column. Our results illustrated this assumption (Figures 3 and 4), and validated the correlation between eye orbit size and diving depths.

References

Debey, Lauren B., and Nicholas D. Pyenson. January 2013. Osteological correlates and phylogenetic analysis of deep diving in living and extinct pinnipeds: What good are big eyes? *Marine Mammal Science,* 29(1): pgs. 48-83.

Eguchi, Tomoharu, and James T. Harvey. April 2005. Diving behavior of the pacific harbor seal (*Phoca vitulina richardii)* in Monterey Bay, California. *Marine Mammal Science,* 21 (2): pgs 283-295.

Gjertz, I., D. Griffiths, B.A. Krafft, C. Lydersen, and O. Wiig. 16 December 2000. Diving and haul-out patterns of walruses *Odobenus rosmarus* on Svalbard. *Polar Biol* 24: pgs. 314-319.

Hanke, Frederike G., Wolf Hanke, Christine Scholtyssek, and Guido Dehnhardt. 25 April 2009. Basic mechanisms in pinniped vision. *Exp. Brain Res*. 199:299-311: pgs 299-311.

Humphries, Stuart, and Graeme D. Ruxton. 15 November 2001. Why did some ichthyosaurs have such large eyes? *The Journal of Experimental Biology* 205: pgs. 439-441.

Jessopp, Mark, Michelle Cronin, and Tom Hart. 7 May 2013. Habitat-mediated dive behavior in free-ranging grey seals. *Plos One* 8(5):pgs. 1-7.

Levenson, David H., and Ronald J. Schusterman. 1999. Dark adaptation and visual sensitivity in shallow and deep-diving pinnipeds. *Marine Mammal Science,* 15(4): pgs. 1303-1313.

Mass, Alla A., and Alexander Ya. Supin. 2007. Adaptive features of aquatic mammals' eye. *The Anatomical Record.* 290: pgs. 701-715.

McDonald, Birgitte I., and Paul J. Ponganis. 19 September 2012. Lung collapse in the diving sea lion: Hold the nitrogen and save the oxygen. *Biology Letters,* 8: pgs. 1047-1049,

Nordoy, Erling S., Lars Folkow, and Arnoldus Schyytte Blix. 1995. Distribution and diving behavior of crabeater seals (*Lobodon carcinophagus)* off Queen Maud Land. *Polar Biology.* 15: pgs. 261-268.

Ollivier, F.J., D. A. Samuelson, D.E. Brooks, P.A. Lewis, M.E. Kallberg, and A.M, Komaromy. 26 January 2004. Comparative morphology of the tapetum lucidum (among selected species). *Veterinary Ophthalmology,* 7(1): pgs. 11-22.

Weise, Michael J., James T. Harvey, and Daniel P. Costa. April 2010. The role of body size in individual-based foraging strategies of a top marine predator. *Ecology* 91 (4): pgs. 1004-1015.