

Commentary

Why did some ichthyosaurs have such large eyes?

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Summary

Many species of extinct marine ichthyosaurs had much larger eyes for their body size than would be expected of extant marine mammals and reptiles. Sensitivity to low light at great depth for the deep-diving genus *Ophthalmosaurus* has recently been suggested as the reason for the large eyes of these animals. Here, we discuss the implications for vision at such depths and consider other optical factors determining eye size. We suggest that

the large eyes of ichthyosaurs are more likely to be the result of simultaneous selection for both sensitivity to low light and visual acuity. The importance of the evolutionary history of extant marine mammals and extinct ichthyosaurs is discussed, as are ecological factors driving both acuity and sensitivity.

Key words: vision, eye size, vertebrate, dive depth, ichthyosaur.

Ichthyosaurs were large marine reptiles that lived between 90 and 250 million years ago. Fossil evidence suggests that several species had very large eyes in comparison with those of the extant dolphins, with which ichthyosaurs are often compared. For example, some 9 m long ichthyosaurs had eyes 25 cm in diameter, more than five times that of similar-sized extant marine mammals. Recently, on the basis of estimating the f -number (see below) of the eye, it has been suggested that the particularly large eyes of the genus *Ophthalmosaurus* allowed it to see in the low light conditions experienced in the sea at depths of at least 500 m (Motani et al., 1999). This depth estimate is similar to those of the dive depth for this genus, based on scaling relationships between size and swimming speed and on size and dive duration in extant diving animals (Motani et al., 1999). Here, we re-evaluate the methods used to obtain these depth estimates and consider the implications of this revision. We suggest that previous estimates may be even more interesting than they first appear.

First, experiments with seals at low light levels suggest that harp seals (*Phoca groenlandica*) are sensitive to different visual images at light levels equivalent to those experienced at a depth of approximately 615 m (Lavigne and Ronald, 1972). In a similar experiment, Wartzok (1979) reported a value of 670 m for spotted seals (*P. largha*). Since seals do not have unusually large eyes compared with those of other mammals, this suggests that ichthyosaurs may well have been able to see at depths substantially greater than 500 m without recourse to enlarged eyes.

The argument that large eyes suggest deep diving is based on the estimation of the f -number of the eye, which is the ratio of the focal length (l_f) of the optical system to the diameter of the aperture (d_a) through which light enters (Denny, 1993). Thus:

$$f = \frac{l_f}{d_a} \quad (1)$$

The sensitivity of the eye (S) changes with f -number to the power -2 :

$$S = \frac{\pi}{4} L \left(\frac{1}{f} \right)^2, \quad (2)$$

where L is the radiance (which is approximately equal to the brightness) of the source. Hence, low f -numbers lead to high sensitivity. We have been able to estimate an f -number for an elephant seal (*Mirounga* spp.) eye and, depending upon assumptions about lens size, we estimate that the minimum f -number for this species is between 1.18 and 1.48 (see Appendix). Motani et al. (1999) estimated the f -number of *Ophthalmosaurus* to be 0.76. Hence, all other things being equal, *Ophthalmosaurus* would have had a sensitivity 2.5–4 times that of an elephant seal. The largest of these values suggests that *Ophthalmosaurus* could probably see in light levels approximately 25% of the minimum requirements of the elephant seal. Surprisingly, this greater sensitivity buys only 42 m of extra depth, since light intensity in the oceans decreases by approximately 90% for every 70 m dropped

(Wartzok and Ketten, 1999). Considering that elephant seals are known to forage at depths of over 1000 m (Schreer and Kovacs, 1996), the comparatively small potential expansion of depth range that large eyes would bring suggests that visual sensitivity alone is insufficient to explain why these ichthyosaurs had huge eyes.

However, we must also be mindful that the method used to estimate the f -number of *Ophthalmosaurus* by Motani et al. (1999) is necessarily indirect and speculative because they were forced to make assumptions based only on preserved skeletal material and not soft tissues. Extant fish, squid and seals, in which we can examine optical systems directly, all have a ratio of focal length to lens radius of approximately 2.5 (Mattheissen's ratio), which equates to an f -number of 1.25 (Land, 1981). The convergence on Mattheissen's ratio through the different evolutionary pathways followed by these groups indicates that 1.25 is likely to be the minimum achievable f -number (Land, 1981). This suggests that the estimate of Motani et al. (1999) of 0.76 for *Ophthalmosaurus* may be a considerable underestimate. However, even if *Ophthalmosaurus* had an f -number of 1.25, it would still have been able to detect light usefully at considerable depths. The human eye, with a fully open pupil, has an f -number of 2.0 (M. F. Land, personal communication) which, all other things being equal, makes it 2.6 times less sensitive than a fish eye. The absolute threshold of the human eye is approximately 10 log units lower than the intensity of sunlight at the ocean surface, meaning that humans are able to see to a depth of approximately 700 m. In comparison, a fish (or *Ophthalmosaurus*) with an f -number of 1.25 and an eye equivalent in size and retinal structure to our own, would be able to see to a depth of perhaps 750 m. Hence, this line of reasoning also suggests that sensitivity to low light levels alone seems unlikely to provide a full explanation for the large eyes of ichthyosaurs.

Sensitivity to low light levels is only one measure of visual ability; another is the ability to resolve fine detail in an image (visual acuity). The resolving power (R) of an eye increases with the focal length of its lens (Bradbury and Vehrencamp, 1998) as:

$$R = \frac{l_f}{2d_r}, \quad (3)$$

where d_r is the centre-to-centre spacing between the receptors of the retina. This introduces a trade-off, since increasing the focal length of the eye on its own increases the f -number and so decreases sensitivity. One way to achieve both good sensitivity and acuity is to allow the focal length to increase, but simultaneously to increase the aperture size to avoid increasing the f -number. Hence, it may be that the large eyes of ichthyosaurs were a result of simultaneous selection for both high sensitivity and acuity. However, it is interesting to note that the visual acuities of extant cetaceans and pinnipeds are generally good and comparable with those of terrestrial hunters such as the domestic cat *Felis catus* (Muir and Mitchell, 1973).

Visual performance also depends on retinal pooling – the

summation of signals from individual sensory cells to produce a retina with fewer individual receptor units but greater sensitivity per receptor. With the longer focal length of its larger eye, an ichthyosaur could pool signals over a much larger region of retina, without loss of acuity, than humans. Alternatively, it could trade off some acuity in return for even greater sensitivity. Land (1981) has suggested that eye size is proportional to the product of resolution and the square root of sensitivity. Hence, increasing resolution by a given factor requires a greater increase in eye size than the same relative increase in sensitivity. This, combined with the impressive visual performance of extant aquatic mammals without huge eyes, suggests that the large eye size of ichthyosaurs was driven by a need for greater visual acuity allied to sensitivity to low light levels. This seems especially likely because the logarithmic decrease in light intensity with depth means that, at depths below 500 m, considerable improvement in sensitivity is required to produce an ecologically relevant increase in the range of visible depths.

However, in terms of visual acuity, the type of receptor cell predominating in the retina strongly influences the value of d_r , as these cells determine the level of receptor pooling. In general, rods tend to pool signals across several neighbouring receptors, thus effectively increasing the value of d_r , while cones generally do not pool. Thus, a predominance of cones in the retina suggests that the value of d_r is relatively small and, hence, that resolution is relatively high (Walls, 1963). This difference can be explained by the function of the two receptor types. Rods are generally found in animals adapted to low light levels, while cones predominate in diurnal species. The phylogenetic history of ichthyosaurs and extant marine mammals indicates that the former were derived from primarily diurnal reptilian ancestors, while mammals are characterised by nocturnal predecessors (Walls, 1963; Muntz, 1978). This suggests that ichthyosaurs had visual systems already geared towards visual acuity more than sensitivity. Pooling of receptor signals in ichthyosaurs would allow increased sensitivity, but at the cost of reduced acuity. Thus, relatively large eyes would appear to be an adaptation for both acuity and sensitivity in these animals.

The above arguments lead us to the conclusion that the ecological demand giving rise to the large eyes of the ichthyosaurs was not simply a need to see in the low light environment of the ocean depths. Rather, large eyes probably developed in response to the constraint of sensitivity, in conjunction with a need for high visual acuity. However, the mechanism driving this need for high visual acuity is not obvious, especially given the good acuity of modern marine mammals. One possible hypothesis is that the main predators and prey of the ichthyosaurs were superficially similar in appearance at a distance, and fine resolution was required to tell one from another at sufficient range to allow flight from predators. However, this is an odd situation apparently not encountered by extant animals, especially considering the body-size scaling relationships involved in predator/prey systems. A more plausible explanation for this need for both

sensitivity and acuity is that these animals were fast, active hunters of small prey at some depth. A similar argument involving the amount of receptor-cell pooling might explain the occurrence of relatively large eyes in many extant cephalopods, such as the giant squid *Architeuthis*, that are fast, deep-swimming hunters. A further possible consequence of selection for high visual acuity is the use of visual signalling or individual recognition between ichthyosaurs, perhaps related to mating or coordinated foraging. It is noticeable that marine animals that do have primarily visual communication (e.g. many cephalopod molluscs, mantis shrimps) also have large eyes relative to their body size.

In summary, we suggest that the large eyes of *Ophthalmosaurus* are the result of simultaneous pressure for sensitivity, allowing prey detection at considerable depths, combined with pressure for high acuity, allowing these animals to hunt small, fast-moving prey.

Appendix

Calculation of elephant seal f-number

Information on gross eye dimensions was taken from Walls (1963). The diameter of the dilated pupil was estimated as 90 % of lens diameter (Motani et al., 1999), which itself was estimated as between 35 and 50 % of the diameter of the eyeball (Walls, 1963). *f*-number was then calculated using the methods of Motani et al. (1999), where the minimum *f*-number was calculated as:

$$f = \frac{0.7 \times (\text{eyeball length})}{(\text{diameter of lens})}. \quad (\text{A1})$$

Further details are given in the Supplementary Information to Motani et al. (1999) at www.nature.com.

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