

A Unique Advantage for Giant Eyes in Giant Squid

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Summary

Giant and colossal deep-sea squid (*Architeuthis* and *Mesonychoteuthis*) have the largest eyes in the animal kingdom [1, 2], but there is no explanation for why they would need eyes that are nearly three times the diameter of those of any other extant animal. Here we develop a theory for visual detection in pelagic habitats, which predicts that such giant eyes are unlikely to evolve for detecting mates or prey at long distance but are instead uniquely suited for detecting very large predators, such as sperm whales. We also provide photographic documentation of an eyeball of about 27 cm with a 9 cm pupil in a giant squid, and we predict that, below 600 m depth, it would allow detection of sperm whales at distances exceeding 120 m. With this long range of vision, giant squid get an early warning of approaching sperm whales. Because the sonar range of sperm whales exceeds 120 m [3–5], we hypothesize that a well-prepared and powerful evasive response to hunting sperm whales may have driven the evolution of huge dimensions in both eyes and bodies of giant and colossal squid. Our theory also provides insights into the vision of Mesozoic ichthyosaurs with unusually large eyes.

Results

Animal eyes range in diameter from below 1 mm in numerous smaller species [1] to the soccer-ball-sized eyes of giant squid. Among vertebrates, the largest eyes are found in whales and large fish. Eye diameters in the blue whale, humpback whale, and sperm whale reach 109 mm, 61 mm, and 55 mm, respectively [2, 6]. Fish generally do not have eyes exceeding a diameter of 90 mm (e.g., swordfish; [7]). Remarkably, the eyes of giant and colossal squid (of the genera *Architeuthis* and *Mesonychoteuthis*) can reach more than two and possibly even three times the diameter of the largest eyes in other animals. There are many anecdotal reports on huge eyes in giant squid and only a few actual measurements, indicating eye diameters from 250 mm to 400 mm [8–11].

Eye size is a fundamental factor determining visual performance [1]. With a larger eye (that can house a larger pupil), diffraction blurring is reduced, and the higher flux of photons allows for smaller contrasts to be detected. But large eyes are expensive to build and maintain [12] and may increase drag or hamper camouflage. These costs must be offset by

the better performance of a larger eye. This reasoning suggests that giant squid need their huge eyes for a visual task that is of unique importance to them and that the performance of this task strongly depends on eye size.

The pelagic habitat is a unique visual world, where downwelling daylight or bioluminescence makes objects visible against a homogeneous background [13–16]. Because of absorption and scattering in water, the contrast between object and background drops dramatically with distance [17], effectively creating a “bubble” of visibility around the observer. Anything of prey size or larger, seen within this bubble, has a large chance of being important, either as a threat or as a potential for food or sex. A major challenge for vision in the pelagic habitat is to detect objects at distances great enough to exploit potential opportunities for beneficial behavioral responses.

Here we report new and well-documented measurements of eye size in both giant and colossal squid and develop a mathematical theory explaining why some deep-sea squid may need giant eyes, when all other animals do well with eyes that are a third the size or smaller.

Confirmation of Eye Size in Giant and Colossal Squid

In a search for more reliable data on the eye size of the largest deep-sea squid, we were fortunate to obtain a photograph of a freshly caught giant squid (*Architeuthis* sp.), where the pupil diameter could be reliably determined to be 90 mm, with the entire eyeball being at least 270 mm (Figure 1). We also had access to an adult colossal squid (*Mesonychoteuthis hamiltoni*) from New Zealand and determined its eye diameter to be between 270 and 280 mm. The colossal squid was the largest individual ever caught, and the mantle width of the giant squid in Figure 1 indicates that it was an adult individual. There is thus reason to believe that eye diameters of about 270 mm are close to the maximum eye size for both *Architeuthis* and *Mesonychoteuthis*. The significantly larger values given by some authors [9, 10] are likely to be exaggerations. But even if we cannot confirm eye diameters much larger than 270 mm, this is still three times the diameter of the largest fish eyes, revealing the huge leap in eye size between giant squid and other animals. If all eyes were serving roughly the same type of visual tasks, such remarkable differences in eye diameter would hardly be expected. Giant and colossal squid share the pelagic depths with a number of large vertebrates whose eyes are just a fraction of the size of those of the squid. This strongly indicates that giant and colossal squid use their eyes for a purpose not shared by other animals.

Theory

Our aim is to identify the main selective pressure underlying the adaptive advantage of uniquely large eyes in deep-sea squid. We approach the problem by developing mathematical expressions relating eye size to visual performance (range of vision) for relevant types of objects and lighting conditions. The objects to be detected are considered to be either bioluminescent point sources or extended objects contrasting against the background space-light. Objects moving through the water are known to trigger bioluminescence in a multitude of

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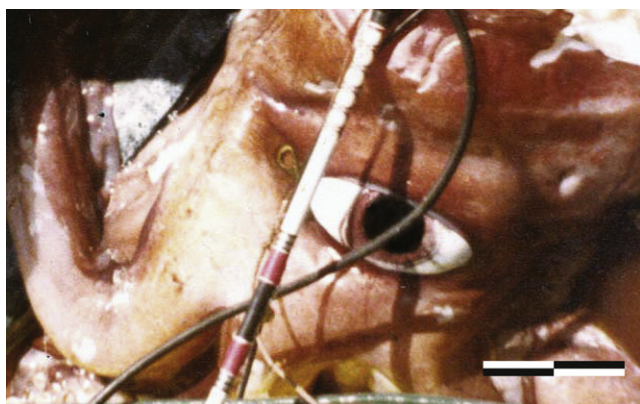


Figure 1. Fresh Head of a Giant Squid with a 90 mm Pupil

The squid was caught on February 10, 1981 by fisherman Henry Olsen about 10 miles offshore from Kahana Bay, Oahu, HI, and the picture was taken by Ernie Choy at the pier. The squid is likely to be of the genus *Architeuthis*. Scale bar represents 200 mm (calibrated by the standard fuel hose across the pupil).

organisms throughout the water column [14, 18–20]. Such stimulated bioluminescence can reveal the moving object either as a number of individually visible point sources or as an extended source without resolution of the individual sources [21].

For extended source detection, we assume an optimum strategy based on dynamic pixels that match the width of the object to be detected (optimal spatial summation [22, 23]), but for point source detection, we assume pixels corresponding to individual photoreceptor cells [16, 23] (Figure 2A). For both point sources and extended objects, detection is a discrimination task where a target pixel has to provide a signal based on the number of detected photons, N_T , that is statistically different from that of an identical reference pixel, N_B , viewing the background next to the target [24], $|N_T - N_B| \geq R\sqrt{N_T + N_B}$, where R is a confidence factor set to 1.96 for 95% confidence [24]. We develop this relationship with expressions for ocean light, water properties, eye geometry, visual optics, and photoreceptor properties and derive equations that relate the pupil diameter to the maximum detection distance (range of vision). The solutions are developed separately for detection of point sources, black extended objects, and luminous extended objects. The resulting equations, their derivations, and notes on the numerical values used for modeling are found in [Supplemental Information](#).

Modeling Visual Range

The theory turns out to be a powerful general tool for analyzing visual strategies in the pelagic habitat. A striking result is that the range of vision, irrespective of depth in the sea, or viewing direction, follows a law of diminishing returns when the eye increases in size (Figure 2B). This phenomenon depends on the absorption and scattering of water and is unique for aquatic vision. The different visual strategies (detection of point sources, black extended objects, and luminous extended objects) follow slightly different curves, but all result in a gradually decreasing performance gain when the eye grows larger. Increasing the eye size gives markedly better vision up to a pupil diameter of about 25 mm. Further increases in eye size become gradually much less rewarding, and this offers a good explanation to why pelagic animals in general

do not have pupil diameters exceeding 30–35 mm. With a typical ratio of about 2.5–3 between focal length and pupil diameter in aquatic eyes [1], this corresponds to eye diameters of about 90 mm, which agrees with the upper bound of eye diameters in fish.

Our modeling clearly demonstrates how the different detection strategies vary with depth in the sea (Figure 2C). In shallow water, extended objects are best detected as dark silhouettes against the brighter space light. But in deep water, the same objects can be seen at long range, in reverse contrast, if the objects trigger plankton bioluminescence as they move through the water. Detection of individual point sources is ineffective in the bright daylight of shallow water but becomes a competitive strategy in the darkness at both moderate and great depths in the sea. However, the situation is more complex than indicated by Figure 2C, because the relative merits of the different viewing strategies also depend on eye size, object size, and viewing direction, as illustrated in Figure 3A. Under most conditions, point source detection provides the longest visual range, except at shallow depths where detection of dark silhouettes is superior, especially for the upward viewing direction where the background is the brightest. The only notable feature that sets very large eyes apart is that they are superior in detecting large luminous objects at depths below about 500 m. The reason for this is that visual contrasts at long range are extremely low and require both a large pupil area and summation over a large target to generate statistically detectable differences between object and background. Thus, the very large eyes of giant squid offer a unique advantage for long-range detection of bioluminescence triggered by large moving objects.

In pelagic animals, the impact that vision has on fitness is likely to be determined not by the detection distance but rather by the water volume the eye can monitor. This is plotted in Figure 3B, and it reveals that, at 600 m or deeper, extended source viewing offers the best performance for detection of predator-size luminous objects through pupil diameters exceeding about 30 mm. Selection driven by this detection strategy may thus favor even larger eyes in animals that already have eyes of substantial size. To analyze how much it pays to increase the eye size, we calculated the increase in visual performance generated by a fractional increase in eye size. The results, summarized in Figure 3C, reveal that the visual strategy providing the best return for eye growth coincides rather well with the best performing visual strategy (Figure 3A). For large eyes, extended viewing of luminous objects is thus not only the best visual strategy for detecting large predators in deep water (Figure 2A), but it is also the strategy that most strongly motivates an increase in eye size. The functions of Figure 3D show that the performance return for increases in eye size from an eye with a 30 mm pupil to one with a 90 mm pupil is uniquely high for the task of detecting objects that are very much larger than the squid itself (predator width, 2 m). For conspecific-size objects or for bioluminescent point sources, the performance return is less than half as good, and for prey-size extended objects, less than 10 times as good as it is for detection of the large, predator-size objects. Extended source viewing of predator-size luminous objects thus offers the unique motivation for huge eyes that we are searching for. A more general interpretation of the calculations is that for dim-light vision in water, low-resolution tasks motivate much larger eyes than high-resolution tasks.

Because our modeling relies on assumptions of a large number of variables, we cannot trust the calculations to be

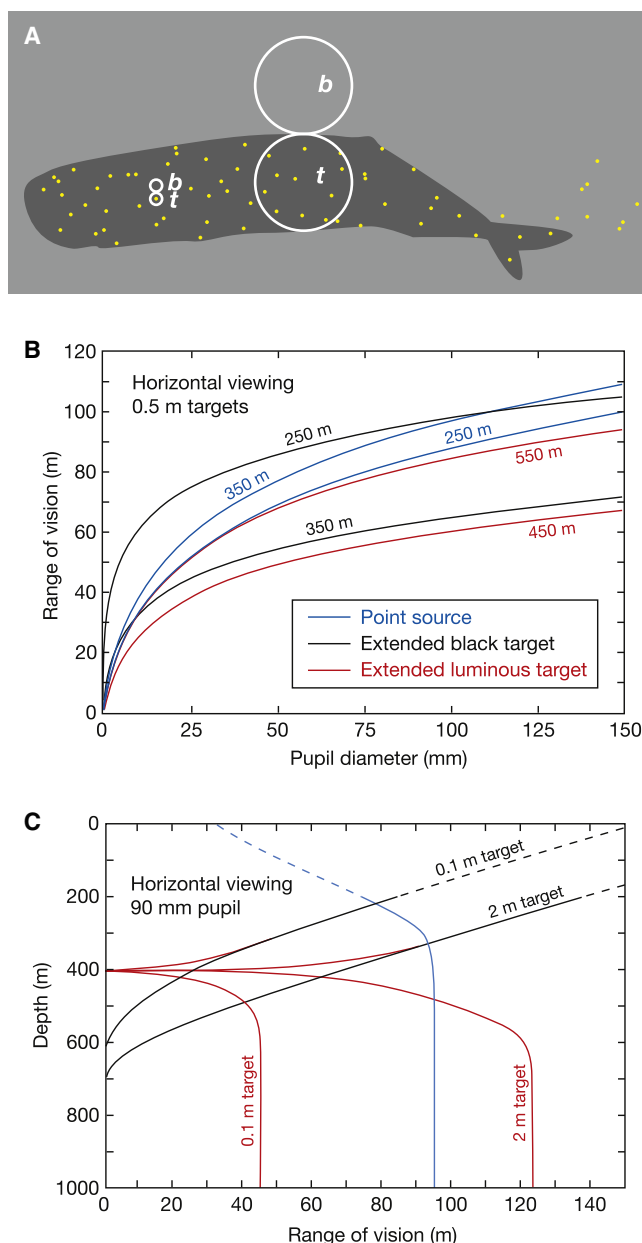


Figure 2. Different Detection Strategies for Pelagic Vision

(A) We analyze the theoretical consequences of target detection in the pelagic world, by finding the limit conditions for discrimination of signals from a target pixel (t) and a background pixel (b). We compare different cases: point source detection of stimulated bioluminescence on the background of a dark object (left) and extended source detection (right) of the same object, against the background space light, both with and without stimulated bioluminescence.

(B) Maximum detection distance, or range of vision, plotted against pupil diameter, showing that the functions for different detection strategies and different depths follow similar laws of diminishing returns for how eye performance increases with eye size. All plots in this figure and in Figure 3 are calculated for clear oceanic water (blue water; see Supplemental Information for details).

(C) Performance of different detection strategies (color coded as in B) as a function of depth in the sea. Here, calculated for the pupil size of a giant squid, it is obvious that detection of extended dark targets, both large (2 m) and small (0.1 m), is a superior strategy in the upper 200–300 m in the ocean, whereas stimulated bioluminescence generated by large moving targets (but not for small ones) offers the longest range of vision at depths below about 500 m. At 400 m depth, the calculations predict that stimulated

entirely faithful to real conditions. However, a sensitivity analysis (see Supplemental Information) reveals that the results are not critically sensitive even to substantial variations in most of the assumed values, and the law of diminishing returns as well as the motivation for very large eyes hold even for significantly different input values. The only variable likely to be critically different to our assumption is the density of bioluminescent organisms, and in areas with only little bioluminescence, the advantage of giant eyes would be diminished.

Discussion

Our calculations clearly indicate that for small eyes, the range of vision increases dramatically with eye size, but for eyes that are already large, the range of vision does not improve much by further increases in eye size. This law of diminishing returns (Figure 2B) is caused by the absorption and scattering of light in water and offers a plausible explanation as to why the eyes of fish do not exceed diameters of about 90 mm (and pupil diameters of about 30 mm). In the record-holding swordfish [7], the head is large enough to house much larger eyes, supporting the conclusion that it is the law of diminishing returns, rather than space constraints, that prevents the development of even larger eyes [25]. The eyes of whales are generally very small compared to their body size [2, 6], and the extremely thick sclera characteristic of whale eyes may account for a third of the diameter. This makes the eye of the blue whale optically smaller than that of swordfish. In agreement with the law of diminishing returns, the eyes of aquatic vertebrates thus display an upper bound of about 90 mm in eye diameter with 30 mm pupils. Although our theory does not point to any specific optimal or maximal eye size, the absence of eyes larger than those of swordfish, in contrast to the rich representation of species covering every eye size below that of swordfish, suggests that the cost of eyes larger than about 90 mm is generally not compensated by the gradually smaller benefit gained by further increases in eye size.

The existence of much larger eyes in giant and colossal squid (three times the diameter of swordfish eyes) would not make much sense if these squid use their eyes for the same purposes as swordfish or any other animal with smaller eyes. Given that giant and colossal squid reach weights similar to that of large swordfish, the eyes are proportionally very much larger in the squid. Although other squid species generally have large eyes for their body size, the allometric growth factor for smaller squid is below 0.7 [26], making the eyes of giant and colossal squid unusually large even for squid.

Objects that are a few meters across that would be of significance to giant squid are of course sperm whales, which are known from their stomach contents to be important predators of giant squid [27, 28]. When sperm whales dive below 500 m in search of squid, they swim continuously [29] and will trigger

bioluminescence balances the darkness of black targets (counter-illumination), rendering targets invisible as extended objects (but still detectable as individual point sources). Values for the upper 200 m (dashed) should be interpreted with caution, because our calculations assume oceanic deep-water clarity, and the upper water layers are often much less clear, which would make the range of vision shorter at these depths. Point source intensities are also chosen for typical mesopelagic bioluminescence, adding to the overestimates of the dashed segment of the blue curve. Downwelling light intensities are calculated from measured values at 200 m depth in oceanic “blue water” during the day. In coastal “green water,” the functions would be compressed up and left.

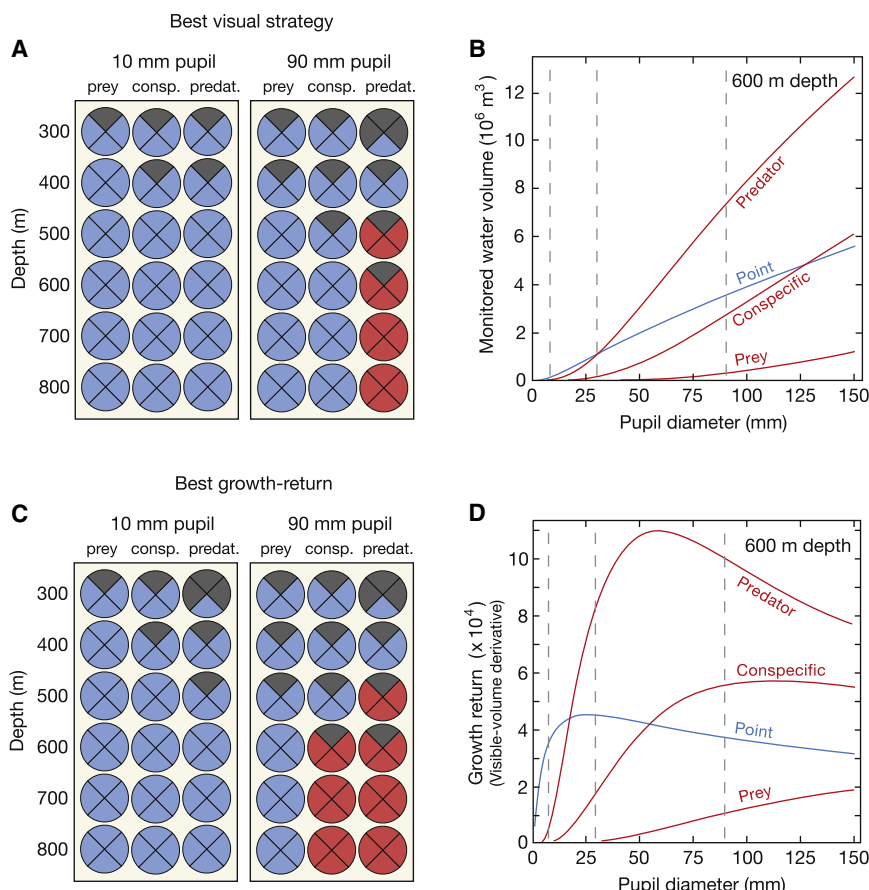


Figure 3. Detection Strategies Offering the Best Visual Performance and Best Return in Response to Increases in Eye Size

(A) Best detection strategy and its dependence on depth in the sea, target size, and viewing direction, for two pupil diameters (10 mm and 90 mm). The color indicates the best detection strategy: blue for point source detection, dark gray for detection of extended black targets, and red for detection of extended luminous targets. The “best” detection strategy is simply the one that provides the longest visibility range for each depth and type of target. The circles are divided into upper and lower quarters for upward and downward viewing and two middle quarters for horizontal viewing. Because the biological meaning of absolute target size depends on the size of the viewer, we have used relative target widths that are scaled to pupil diameter, such that for a 90 mm pupil, a prey is 0.1 m, a conspecific is 0.5 m, and a predator is 2 m. For smaller eyes, the targets are then proportionally smaller. The only feature that qualitatively sets the giant eye apart is its ability to use extended source vision to detect luminous predator-size objects at long range in deep water.

(B) Example of curves used for finding the best detection strategies, here for horizontal viewing at 600 m depth. Visual performance (y axis) has been calculated here as monitored water volume rather than the visual range used in Figure 2A. Point source detection is clearly the best strategy for eyes with pupil diameters up to about 30 mm, but for further increases in eye size, predator-size objects rapidly become much better detected as extended luminous objects (vertical dashed lines indicate pupil diameters of 10, 30, and 90 mm).

(C and D) Illustrations of the performance return generated by increases in eye size. For a 30 mm

pupil (data not shown), (C) (and also A) would essentially be identical to the diagram for a 10 mm pupil, but for pupils above 30 mm, the results gradually approach the conditions shown for 90 mm pupils. There is a striking correlation between best performance in (A) and best return for growth in (C). The derivative functions in (D) further show that at pupil diameters above 30 mm, where extended source detection is superior for predator detection, this strategy gains more than twice as much from increases in eye size as the other detection strategies or target sizes. The values plotted in (D) are calculated as the derivative of functions like those in (B), or more precisely, the relative gain in detection range divided by relative increase in pupil diameter. The values on the y axis thus indicate to which proportion detection range increases when the eye is allowed to grow by a small fraction. Color codes for the different curves in (B) and (D) are as in Figure 2, but black traces (for black extended targets) are omitted because they do not rise noticeably above the x axes.

bioluminescence in the small organisms they disturb [14], and because giant and colossal squid have such huge eyes, they will see this light at a distance of about 120 m in areas of sufficient bioluminescence. For this particular task, the law of diminishing returns is replaced by a superior performance gain for increased eye size in the range from 90 mm to 300 mm (pupil diameters 30–100 mm, Figure 3D). For other visual tasks, such as detection of prey or conspecifics, the huge eyes offer only marginally better performance compared to smaller and much more economic eyes. Strong arguments against point source detection providing the main selective advantage for very large eyes is that isolated point sources at long range (>90 m; Figure 2C) would be biologically irrelevant, and for larger aggregations of point sources, extended source detection is more efficient (Figures 3A and 3B). Earlier modeling [16] has also concluded that efficient point source detection only requires a very modest eye size. We thus conclude that the most likely explanation for the unusually large eyes in giant and colossal squid is the unique ability to detect large predators that trigger plankton bioluminescence as they move through the water.

Pelagic bioluminescence can however be extremely patchy, with large variations in the abundance and intensity of

bioluminescent organisms [13, 14, 18, 30]. The advantage of giant eyes for long-range detection of large predators will clearly exist only as long as the squid stay in locations where bioluminescent plankton is reasonably abundant. But it is possible that the squid actively position themselves in such areas where they may be more likely to encounter food and can improve their chances of detecting approaching predators. Such a preference would also increase their chances of encountering mates. However, significant levels of spontaneous bioluminescence are virtually nonexistent [18], and bioluminescence-rich areas may be difficult to find visually unless disturbed by larger animals. Also, the body constitution of both giant and colossal squid suggests that they are ambush predators that are not continuously in motion [8, 10], and as such, they would themselves not normally trigger much plankton bioluminescence.

A long detection range implies that a huge water volume around the squid can be monitored for predators (7 million m^3 , assuming a sphere defined by the 120 m visual range). Sperm whales, in contrast, are likely to rely on their sonar to detect squid. Their sonar range is a couple hundred meters for detecting small squid [3, 31] and presumably longer for detecting larger prey. Squid are deaf to the high frequency sonar

clicks of toothed whales [32, 33], leaving vision their only option for detecting distant approaching predators. Despite their huge eyes, giant and colossal squid are thus unlikely to spot a sperm whale before being revealed by the whale's sonar. This argument implies that the main advantage of giant eyes is not to be able to move out of the whale's detection range but rather to provide enough time to prepare for an effective evasive response. The large body required to build, sustain, and propel a pair of soccer-ball-sized eyes may also offer enough physical power to benefit from the early visual warning and allow for a suitably timed and forceful escape behavior. It is thus possible that predation by large toothed whales has generated a combined selection driving the evolution of gigantism in both bodies and eyes of these squid.

A group of extinct marine reptiles, the ichthyosaurs, are the only other animals known to have had eyes that were similar in size to those of giant squid [34]. Contrary to previous belief [34, 35], our arguments suggest that also in ichthyosaurs the giant eyes were adaptations for low-resolution tasks in dim light. But ichthyosaur ecology clearly must have differed from that of giant squid. Ichthyosaurs were not built for ambush predation but had bodies suggesting that they were capable of sustained high-speed cruising, much like present-day swordfish. Unfortunately, the fossils do not indicate whether they were day or night active, but they are thought to have dived to mesopelagic depths [34]. A general conclusion from our modeling is that the large ichthyosaur eyes (34–35 cm in diameter), just like giant squid eyes, had a significant selective advantage only for detection of large extended targets in dim light. For other visual tasks, much smaller (and less energetically expensive) eyes perform almost as well.

Ichthyosaurs lived in the mid-Triassic to mid-Cretaceous, long before the first whales evolved, and would presumably have used their large eyes for spotting other large objects. Interestingly, giant plesiosaurs lived in the sea during much the same period as ichthyosaurs, and genera such as *Kronosaurus* and *Rhomaleosaurus* were massive apex predators [36] that may have posed a threat to ichthyosaurs. Some of the large-eyed ichthyosaurs were massive animals themselves, such as *Temnodontosaurus* [37], suggesting the possibility that seeing each other in dim light was of crucial importance. Our modeling (Figure 3D) offers the least support for the development of huge eyes for spotting prey. This argument is supported by the laterally pointing eyes [34] and the lack of an aphakic gap for improved forward vision in *Temnodontosaurus*, as judged from the circular sclerotic rings [37]. It seems more likely that the visual targets of main interest to these giant ichthyosaurs could appear in any direction.

The computational approach to vision that we introduce in this paper is useful not only for revealing possible reasons for exceptionally large eyes in squid and ichthyosaurs but also for investigating numerous other aspects of visual ecology in aquatic habitats. For depths that are largely inaccessible to humans, modeling of visual performance offers a unique way to investigate how animals can interact visually and specialize their visual system to different detection strategies. The theoretical framework developed here can be adapted to approach questions of visual ecology in any aquatic habitat from the bathypelagic to freshwater ponds.

Supplemental Information

Supplemental Information includes Supplemental Theory and can be found with this article online at [doi:10.1016/j.cub.2012.02.031](https://doi.org/10.1016/j.cub.2012.02.031).

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References

- Land, M.F., and Nilsson, D.-E. (2002). *Animal Eyes* (Oxford, New York: Oxford University Press).
- Walls, G.L. (1942). *The Vertebrate Eye and Its Adaptive Radiation* (Bloomfield Hills: Cranbrook).
- Möhl, B., Wahlberg, M., Madsen, P.T., Heerfordt, A., and Lund, A. (2003). The monopulsed nature of sperm whale clicks. *J. Acoust. Soc. Am.* 114, 1143–1154.
- André, M., Johansson, T., Delory, E., and van der Schaar, M. (2007). Foraging on squid: the sperm whale mid-range sonar. *J. Mar. Biol. Assoc. U. K.* 87, 59–67.
- Beedholm, K., and Möhl, B. (2006). Directionality of sperm whale sonar clicks and its relation to piston radiation theory. *J. Acoust. Soc. Am.* 119, EL14–EL19.
- Howland, H.C., Merola, S., and Basarab, J.R. (2004). The allometry and scaling of the size of vertebrate eyes. *Vision Res.* 44, 2043–2065.
- Fritsches, K.A., Brill, R.W., and Warrant, E.J. (2005). Warm eyes provide superior vision in swordfishes. *Curr. Biol.* 15, 55–58.
- Roper, C.F.E., and Boss, K.J. (1982). The giant squid. *Sci. Am.* 246, 96–105.
- Akimushkin, I.I. (1963). *Cephalopods of the Seas of the USSR* (in Russian). Izdatel'stvo Akademii Nauk SSSR. Moscow (Jerusalem, 1965: Israel Program for Scientific Translation).
- Ellis, R. (1998). *The Search for the Giant Squid* (New York: The Lyons Press).
- Kubodera, T., and Mori, K. (2005). First-ever observations of a live giant squid in the wild. *Proc. Biol. Sci.* 272, 2583–2586.
- Laughlin, S.B., de Ruyter van Steveninck, R.R., and Anderson, J.C. (1998). The metabolic cost of neural information. *Nat. Neurosci.* 1, 36–41.
- Herring, P.J. (2002). *The Biology of the Deep Ocean* (Oxford, New York: Oxford Univ Press).
- Widder, E.A. (2001). Bioluminescence and the pelagic visual environment. *Mar. Freshwat. Behav. Physiol.* 35, 1–26.
- Nilsson, D.-E. (1996). Eye design vision and invisibility in planktonic invertebrates. In *Zooplankton: Sensory Ecology and Physiology*, P.H. Lenz, D.K. Hartline, J.E. Purcell, and D.L. Macmillan, eds. (Amsterdam: Gordon and Breach Publishers), pp. 149–162.
- Warrant, E.J., and Locket, N.A. (2004). Vision in the deep sea. *Biol. Rev. Camb. Philos. Soc.* 79, 671–712.
- Mertens, L.E. (1970). *In-Water Photography: Theory and Practice* (New York: John Wiley & Sons).
- Widder, E.A., and Johnsen, S. (2000). 3D spatial point patterns of bioluminescent plankton: a map of the 'minefield'. *J. Plankton Res.* 22, 409–420.
- Herring, P.J. (1998). Dolphins glow with the flow. *Nature* 393, 731–733.
- Rohr, J., Latz, M.I., Fallon, S., Nauen, J.C., and Hendricks, E. (1998). Experimental approaches towards interpreting dolphin-stimulated bioluminescence. *J. Exp. Biol.* 201, 1447–1460.
- Johnsen, S., Widder, E.A., and Mobley, C.D. (2004). Propagation and perception of bioluminescence: factors affecting counterillumination as a cryptic strategy. *Biol. Bull.* 207, 1–16.
- Warrant, E.J. (1999). Seeing better at night: life style, eye design and the optimum strategy of spatial and temporal summation. *Vision Res.* 39, 1611–1630.
- Warrant, E.J. (2008). Nocturnal vision. In *The Senses: A Comprehensive Reference*, R.R. Hoy, G.M. Shepherd, A.I. Basbaum, A. Kaneko, and G. Westheimer, eds. (Oxford: Academic Press), pp. 53–86.

24. Land, M.F. (1981). Optics and vision in invertebrates. In Handbook of Sensory Physiology, Vol. VIII/6B, H. Autrum, ed. (Berlin, Heidelberg, New York: Springer), pp. 471–592.
25. Kröger, R.H.H., Fritsches, K.A., and Warrant, E.J. (2009). Lens optical properties in the eyes of large marine predatory teleosts. J. Comp. Physiol. A Neuroethol. Sens. Neural Behav. Physiol. 195, 175–182.
26. Zeidberg, L.D. (2004). Allometry measurements from *in situ* video recordings can determine the size and swimming speeds of juvenile and adult squid *Loligo opalescens* (Cephalopoda: Myopsida). J. Exp. Biol. 207, 4195–4203.
27. Clarke, M.R., Martins, H.R., and Pascoe, P. (1993). The diet of sperm whales (*Physeter macrocephalus* Linnaeus 1758) off the Azores. Philos. Trans. R. Soc. Lond. B Biol. Sci. 339, 67–82.
28. Clarke, M.R. (1996). Cephalopods as prey. III. Cetaceans. Phil. Trans. Biol. Sci. 351, 1053–1065.
29. Davis, R.W., Jaquet, D., Gendron, D., Markaida, U., Bazzino, G., and Gilly, W. (2007). Diving behavior of sperm whales in relation to behavior of a major prey species, the jumbo squid, in the Gulf of California, Mexico. Mar. Ecol. Prog. Ser. 333, 291–302.
30. Widder, E.A., Johnsen, S., Bernstein, J.F., Case, J.F., and Neilson, D.J. (1999). Thin layers of bioluminescent copepods found at density discontinuities in the water column. Mar. Biol. 134, 429–437.
31. Madsen, P.T., Wilson, M., Johnson, M., Hanlon, R.T., Bocconcelli, A., Aguilar de Soto, N., and Tyack, P.L. (2007). Clicking for calamari: toothed whales can echolocate squid *Loligo pealeii*. Aquat. Biol. 1, 141–150.
32. Wilson, M., Hanlon, R.T., Tyack, P.L., and Madsen, P.T. (2007). Intense ultrasonic clicks from echolocating toothed whales do not elicit anti-predator responses or debilitate the squid *Loligo pealeii*. Biol. Lett. 3, 225–227.
33. Mooney, T.A., Hanlon, R.T., Christensen-Dalsgaard, J., Madsen, P.T., Ketten, D.R., and Nachtigall, P.E. (2010). Sound detection by the longfin squid (*Loligo pealeii*) studied with auditory evoked potentials: sensitivity to low-frequency particle motion and not pressure. J. Exp. Biol. 213, 3748–3759.
34. Motani, R., Rothschild, B.M., and Wahl, W. (1999). Large eyeballs in diving ichthyosaurs. Nature 402, 747.
35. Humphries, S., and Ruxton, G.D. (2002). Why did some ichthyosaurs have such large eyes? J. Exp. Biol. 205, 439–441.
36. Smith, A.S., and Dyke, G.J. (2008). The skull of the giant predatory plesiosaur *Rhomaleosaurus cramptoni*: implications for plesiosaur phylogenetics. Naturwissenschaften 95, 975–980.
37. McGowan, C. (1994). *Temnodontosaurus risor* is a juvenile *T. platyodon* (Reptilia: Ichthyosauria). J. Vertebr. Paleontol. 14, 472–479.