

Report

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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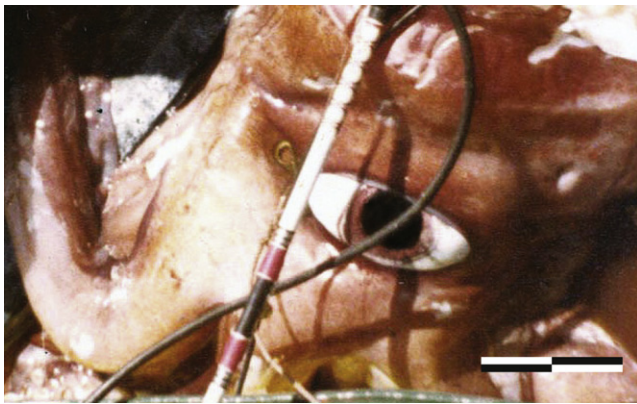


Figure 1. Fresh Head of a Giant Squid with a 90 mm Pupil

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

Why Giant Squid Have Giant Eyes

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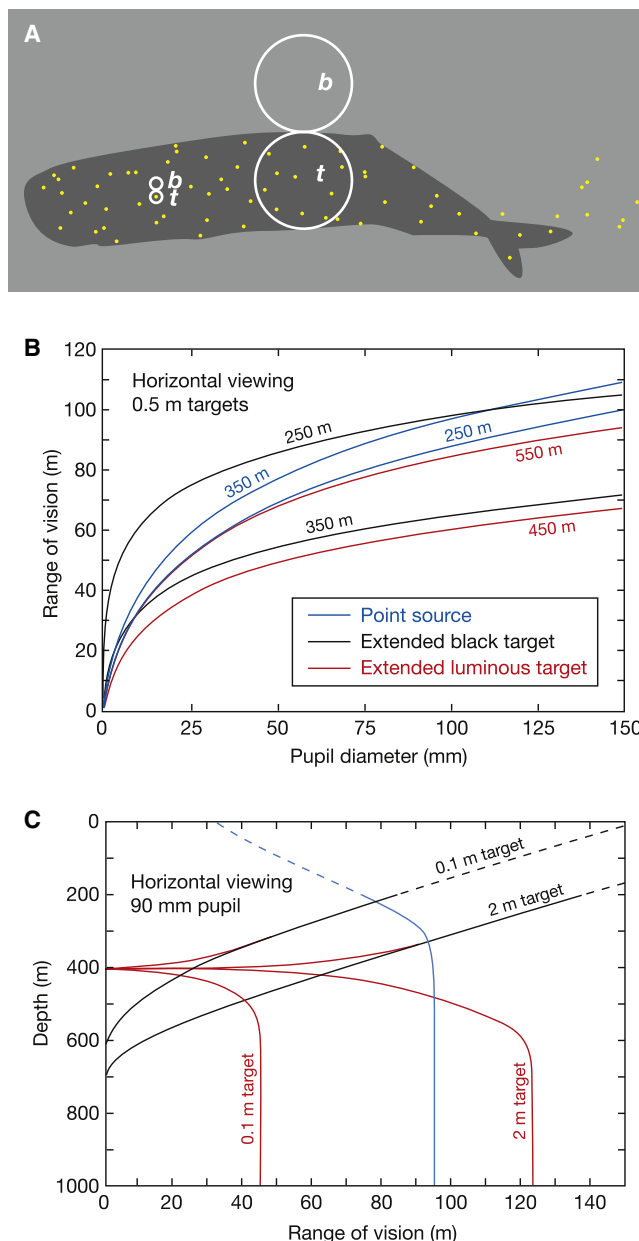


Figure 2. Different Detection Strategies for Pelagic Vision

(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.

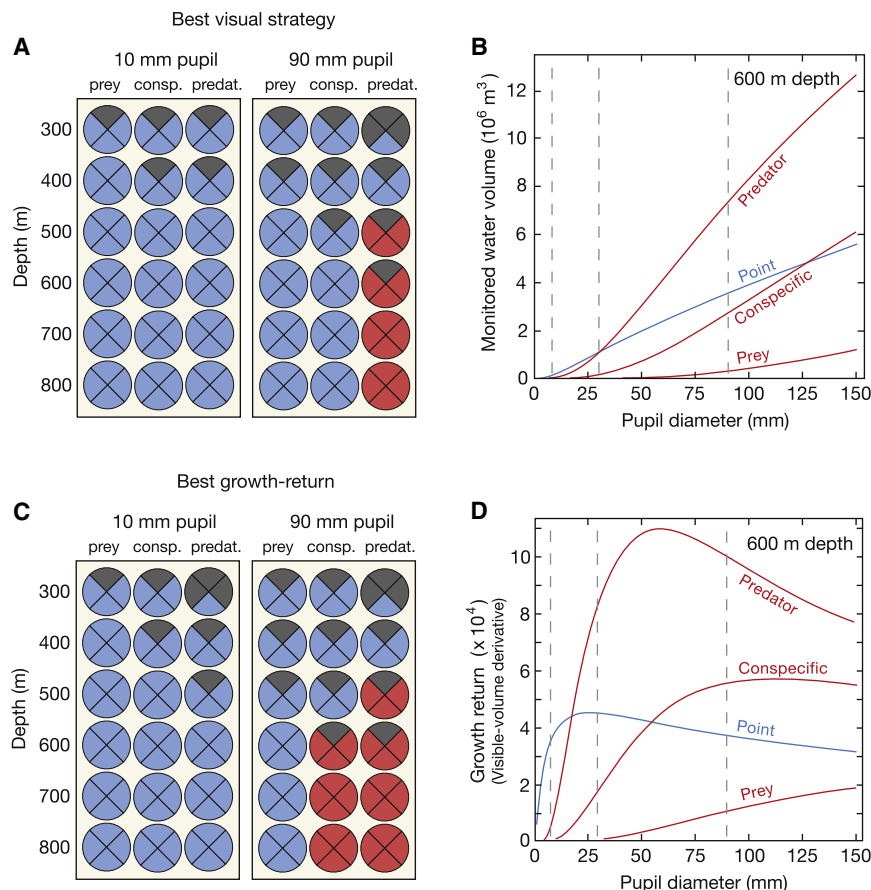


Figure 3. Detection Strategies Offering the Best Visual Performance and Best Return in Response to Increases in Eye Size

(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.

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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.

A Unique Advantage for Giant Eyes in Giant Squid

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Supplemental Theory

Discrimination criteria Detection of a target against a background requires discrimination of signals from visual channels sampling light from the target and the background respectively. We assume that the channels being compared have identical properties. A target channel detects a mean of N_T photons per integration time, and the corresponding mean count for a background channel is N_B . The photon counts are sums of real photons and intrinsic noise. We follow Land [24] and assume Gaussian distribution of photon samples. Discrimination between the signals in the two channels is possible when the difference is greater than or equal to a reliability constant R times the standard deviation of the difference (which is the square root of the sum of the two means; see Land [24]: $|N_T - N_B| \geq R\sqrt{N_T + N_B}$). The discrimination threshold is then given by:

$$|N_T - N_B| = R\sqrt{N_T + N_B} \quad \text{Eq. 1}$$

Variables and constants are defined in the Table on page 5. For confidence levels and values of R see the Table on page 6.

Case 1: Detection of a point-source on a black target We assume a pair of visual channels optimally suited to discriminate a point source against a dimmer background. A target channel is aimed at the bioluminescent point source, and its signal is compared to that of a channel aimed at the background next to the point source (Fig. 2A). The target channel is assumed to receive all light that enters the eye from the bioluminescent point source. For both channels, the target blocks background space-light from behind the target, but new space-light is scattered into the line of sight between the target and the observer. The target channel will receive an average of N_{bio} photons per integration time from the point source and N_{black} photons scattered in along the line of sight, whereas the background channel only receives N_{black} photons from the line of sight. Each channel also generates an average of X_{ch} false photons per integration time. The total average signal in the target channel will thus be $N_T = N_{bio} + N_{black} + X_{ch}$ and in the background channel, $N_B = N_{black} + X_{ch}$. Inserting this into Eq. 1 gives:

$$N_{bio} = R\sqrt{N_{bio} + 2N_{black} + 2X_{ch}}. \quad \text{Eq. 2}$$

Before we derive expressions for N_{bio} and N_{black} , we need to consider the angular size of the two channels. We know that aquatic eyes typically have focal lengths of 2.55 lens radii [1] (Matthiessen's ratio, $M=2.55$). Expressed in pupil diameters (A), the focal length, f , is $0.5MA$, and the angular diameter of the Airy disc becomes $2.44\lambda M / 2nf$ radians. Multiplied by the focal length to get the actual size on the retina we get $2.44\lambda M / 2n$. This means that if M is constant, the diffraction blur spot has a constant size on the retina irrespective of eye size. For a wavelength (λ) of 480 nm, a refractive index (n) of 1.33, and $M = 2.55$ the Airy disc is 1.1 μm , and for M as high as 3, the Airy disc is still only 1.3 μm . But photoreceptor diameters in giant squid are larger (5 μm), which implies that realistic angular dimensions of the spatial channels should be given by the actual receptor diameter. We assume a Gaussian profile of the angular sensitivity of the receptor [S1], where the half-width is d/f (radians) and its solid angle is $1.13(d/f)^2$ (steradians).

We are interested in the relation between the pupil diameter A and the range r , and search for expressions relating these to N_{bio} and N_{black} . Following Warrant [S2], light divergence from an isotropic point source of bioluminescence gives a photon flux density of $E/4\pi r^2$, attenuation by water is given by $e^{-\alpha r}$ and the pupil area accepting the light is $\pi A^2/4$. The product of these factors multiplied by the efficiency of the retina and the integration time provides the desired expression of N_{bio} (see the Table on page 5 for explanation of variables):

$$N_{bio} = \frac{EA^2}{16r^2} e^{-\alpha r} q \Delta t \quad \text{Eq. 3}$$

The space-light is an extended source, and the sensitivity [1] of a retinal channel is simply the product of the pupil area, $\pi (A/2)^2$, the solid angle in visual space of the channel, $1.13(d/f)^2$, and the efficiency q by which the eye detects photons. For an observer at constant depth in the sea, space-light enters the line of sight at the rate $1 - e^{-(\kappa-\alpha)r}$, where κ depends on the viewing angle [17, S3]. The radiance seen in the direction of a black target then becomes $I_{space}(1 - e^{-(\kappa-\alpha)r})$, where I_{space} is the background radiance at the depth of the observer. We arrive at N_{black} by multiplying the sensitivity by the radiance and the integration time Δt :

$$N_{black} = 1.13 \left(\frac{\pi}{4} \right) A^2 \left(\frac{d}{f} \right)^2 q \Delta t \cdot I_{space} (1 - e^{-(\kappa-\alpha)r}). \quad \text{Eq. 4}$$

We know from above that $f = (M \cdot A)/2$ and get:

$$N_{black} = 3.55 \left(\frac{d}{M} \right)^2 q \Delta t \cdot I_{space} (1 - e^{-(\kappa-\alpha)r}). \quad \text{Eq. 5}$$

The dark noise per integration time is simply:

$$X_{ch} = X \Delta t. \quad \text{Eq. 6}$$

We now combine Eqs. 3, 5 and 6 with Eq. 2, and solve for A to obtain the desired relation for detection of point sources:

$$A = \sqrt{R^2 \left(1 + \sqrt{1 + \frac{8 \left(3.55 \left(\frac{d}{M} \right)^2 q \Delta t \cdot I_{space} (1 - e^{(\kappa - \alpha)r}) + X \Delta t\right)}{R^2}} \right) \frac{8r^2}{Eq \Delta t} e^{\alpha \cdot r}} \quad \text{Eq. 7}$$

Cases 2 and 3: Detection of an extended black target, and an extended luminous target

We again assume an equal pair of visual channels, but now optimally sized to detect an extended object against the background space-light. To maximise the signal, the target channel fills the width of the object (Fig. 2A), and both channels have square rather than Gaussian sensitivity profiles. We thus assume that the angular size of the visual channels is dynamic, and suited to the object at all times. The angle in visual space of such a channel is the target width divided by its distance, T/r (radians), and with a square profile its solid angle is $(\pi/4)(T/r)^2$ (steradians). The channel is formed as a circular pool of photoreceptors, where each photoreceptor occupies a solid angle of $(\pi/4)(d/f)^2$ in visual space (see the Table on page 5 for definition of variables). The number of photoreceptors forming a channel is then $(Tf/rd)^2$, and its diameter on the retina is Tf/r .

The target itself is assumed to be black (zero reflectance), but as it moves through the water it may trigger bioluminescent flashes within its profile, but not in the visual field of the background channel. The signal of the target channel comes from target bioluminescence attenuated on its way to the eye, space-light having entered the line of sight between the target and the eye, and dark noise from the contributing photoreceptors: $N_T = N_{bio} + N_{black} + X_{ch}$, and the background channel sums background space-light and channel noise: $N_B = N_{space} + X_{ch}$. The discrimination threshold from Eq. 1 now becomes

$$|N_{bio} + N_{black} - N_{space}| = R \sqrt{N_{bio} + N_{black} + N_{space} + 2X_{ch}} \quad \text{Eq. 8}$$

We are now ready to work out expressions for N_{bio} , N_{black} , N_{space} and X_{ch} , which happens to be easier in the reverse order. Note that the signal parameters used in this case will have to be derived anew, because they are not identical to those derived for the point source case. The channel noise X_{ch} is derived as for the point source case, but here multiplied by the number of photoreceptors in the pool, and combined with the relation $f = MA/2$:

$$X_{ch} = \left(\frac{TMA}{2rd} \right)^2 X \Delta t. \quad \text{Eq. 9}$$

The background detector is now directly monitoring the unblocked spacelight I_{space} . To arrive at the photon count of the detector, we put together factors corresponding to those used for Eq. 4,

but with T/r replacing d/f , and assuming a square rather than Gaussian profile of the angular sensitivity (replacing 1.13 with $\pi/4$):

$$N_{space} = \left(\frac{\pi}{4}\right)^2 A^2 \left(\frac{T}{r}\right)^2 q\Delta t \cdot I_{space} = 0.617 A^2 \left(\frac{T}{r}\right)^2 q\Delta t \cdot I_{space}. \quad \text{Eq. 10}$$

The amount of detected light entering the line of sight between the target and the eye, N_{black} , can be worked out by replacing I_{space} of Eq. 10 with $I_{space} \left(1 - e^{(\kappa - \alpha)r}\right)$ as in Eq. 4:

$$N_{black} = 0.617 A^2 \left(\frac{T}{r}\right)^2 q\Delta t \cdot I_{space} \left(1 - e^{(\kappa - \alpha)r}\right) \quad \text{Eq. 11}$$

Bioluminescence triggered by the target is likely to be composed of randomly distributed point sources. With the mean distance x between nearest neighbours, the number of point sources per unit area of the target is $1/(4x^2)$ [S4]. The product of this density and the area viewed by the target channel, $(\pi/4)T^2$, yields the total number of point sources seen by the target channel: $\pi \cdot T^2/16x^2$. We can now multiply the expression of Eq. 3 with the number of viewed point sources to obtain N_{bio} for the extended source case:

$$N_{bio} = \frac{\pi \cdot T^2 E A^2}{256 x^2 r^2} e^{-\alpha \cdot r} q\Delta t \quad \text{Eq. 12}$$

This expression also holds for small targets seen at long distances, because the modulation transfer function of deep oceanic water is practically flat from zero spatial frequency up to 10 cycles per degree [21]. We can thus safely ignore effects caused by spatial degradation of the image.

We now substitute Eqs. 9-12 for X_{ch} , N_{space} , N_{black} and N_{bio} in Eq. 8 and solve for A to obtain:

$$A = \frac{R \sqrt{q\Delta t \left\{ \frac{\pi \cdot T^2 E}{256 x^2 r^2} e^{-\alpha \cdot r} + 0.617 \left(\frac{T}{r}\right)^2 \left[I_{space} \left(2 - e^{(\kappa - \alpha)r} \right) \right] \right\} + 2 \left(\frac{TM}{2rd}\right)^2 X\Delta t}}{\left| q\Delta t \left\{ \frac{\pi \cdot T^2 E}{256 x^2 r^2} e^{-\alpha \cdot r} - 0.617 \left(\frac{T}{r}\right)^2 \left[I_{space} \left(e^{(\kappa - \alpha)r} \right) \right] \right\} \right|}, \quad \text{Eq. 13}$$

which is the desired relation between A and r for detection of extended sources. The visibility of non-luminous extended black targets (dark silhouettes) can also be analysed by Eq. 13, simply by allowing $E = 0$.

Definition of variables (units in brackets)

N_T	Mean number of real and false photons detected per integration time in a visual channel aimed at the target (photons)
N_B	Mean number of real and false photons detected per integration time in a visual channel viewing the background space-light (photons)
N_{bio}	Mean photon count (per integration time) originating from bioluminescent sources (photons)
N_{space}	Mean photon count (per integration time) from background space-light (photons)
N_{black}	Mean photon count (per integration time) originating from light scattered into the line of sight between target and observer (photons)
X_{ch}	Number of false photons (dark noise) per integration time in a visual channel (photons)
X	Dark noise rate per photoreceptor (photons s ⁻¹)
A	Pupil diameter (m)
r	Range: maximum visibility distance to target (m)
E	Number of photons emitted by bioluminescent point source in all directions per second (photons s ⁻¹)
I_{space}	Radiance of space-light background in the direction of view at the position (depth) of the eye (photons m ⁻² s ⁻¹ sr ⁻¹)
T	Width of extended target (m)
x	Average distance between point sources across an extended object (m)
α	Beam attenuation coefficient of sea water (m ⁻¹)
κ	Attenuation coefficient of background radiance (backscattering coefficient) (m ⁻¹)
λ	Wavelength of light, taken as 480 nm for bioluminescence and transmitted daylight
n	Refractive index in object and image space, taken as the value for water, 1.33
d	Photoreceptor diameter (m)
Δt	Integration time (s)
q	Detection efficiency: ratio of detected to incident photons, which depends on losses in the ocular media, the fraction absorbed by photopigment and the transduction efficiency
f	Focal length (m)
M	Matthiessen's ratio, $2f/A$
R	Reliability coefficient

Values assumed for modelling We used values that in our opinion are the most realistic (see Table on this page). Values for radiance of down-welling daylight, and absorption in the sea are based on measurements in oceanic water [21]. The original data come from Dr Andrew Barnard, Dr Scott Pegau and Dr Ronald Zaneveld (College of Oceanic and Atmospheric Sciences, Oregon State University, Corvallis, OR, USA), who collected them using a dual path, multiband absorption/ attenuation meter (ac-9, Wetlabs Inc.) and fluorometer in the Equatorial Pacific (10.05 local time, 30 April 1996; 0°0_ N, 177°21_ W). Absorption and beam attenuation coefficients (at 412, 440, 488, 510, 532, 555, 650 and 676 nm) and chlorophyll concentration were measured at 1 m intervals to a depth of 199 m (after which depth inherent optical properties and chlorophyll concentration values were assumed to remain constant). These values were then input into a radiative transfer software package to compute the relevant radiances and irradiances as a function of depth. The energy values per nm were converted to quanta, and the number of photons available to photoreceptors was spectrally integrated over 390-510 nm using a spectral sensitivity curve calculated for 300 μm long *Architeuthis* photoreceptors from a rhodopsin template [S5] peaking at 470 nm. At a depth of 200m the number of quanta (per m^2 , s and sr) was $6.28 \cdot 10^{15}$ for down-welling radiance, $5.11 \cdot 10^{13}$ for horizontal radiance and $2.90 \cdot 10^{13}$ for up-welling radiance. Below 200 m the log radiances decrease linearly with depth, and the intensity reduction per 100 m was 1.638 log units for down-welling radiance, 1.677 log units for horizontal radiance and 1.668 log units for up-welling radiance. The attenuation and backscatter coefficients for 488 nm were assumed constant below 200 m, with $\alpha = 0.0468$, and $\kappa = 0.0385$ for looking up, $\kappa = 0$ for horizontal viewing, $\kappa = -0.0385$ for looking downwards.

Rhabdom diameters ranging between 5 and 6 μm in an *Arciteuthis* sp. (mantle length 1.43 m, caught on December 4, 2006) were measured from semi-thin sections of a central piece of retina embedded in histological Araldite. The piece of retina was prepared from an eye preserved in 4% formalin, and kindly put at our disposal by Dr Tsunemi Kubodera.

Video recordings of live *Architeuthis* [11] together with typical foraging depths of sperm whales [S6, S7], suggest that giant squid normally inhabit depths of 600-1000 m during the day. A recent investigation [S8] indicates occasional presence at moderate depths (200-400 m).

List of values used for modelling

R	1.96 for 95% confidence [24]
E	$1 \cdot 10^{11}$ quanta s^{-1} for gelatinous zooplankton [S2, 14, S9]
x	0.3 m assumed for gelatinous zooplankton [18]; can be much smaller in dinoflagellate and copepod layers of shallow water)
T	0.1 m for prey; 0.5 m for conspecific; 2 m for predator (sperm whale)
d	5 μm (measured histologically in <i>Architeuthis</i> sp., see above)
Δt	0.16 s (mysid) [S10, S11]
q	0.36 [S12]
X	$1 \cdot 10^{-4}$ s^{-1} [14, 16]
M	2.55 [S13]

Sensitivity analysis Apart from the values given in the Table on page 6, we also used alternative values to test if the conclusions were critically sensitive to variations in variables within reasonable bounds. The Table below list alternative values and the effect these have on three cases, taken from the traces presented in Fig 2B. We also tested the alternative values from the Table below on all diagrams presented in the paper (Figs. 2B, C and 3A-D), and found that the conclusions of the investigation are surprisingly robust, and remain valid for each individual substitution of alternative values. We also analysed the effect of random variation of input values, within the tabulated ranges, and confirmed that large extended targets provide the best growth return under all permutations of possible input values (Figure 3 C, D).

Alternative values and their consequence in % of the calculated visual range

		Detection principles and conditions		
		Point source A=50 mm 350 m depth horizontal viewing	Extended dark A=50 mm 250 m depth horizontal viewing 0.5 m target	Extended luminous A=50 mm 550 m depth horizontal viewing 0.5 m target
<i>E</i>	1·10 ⁹ dinoflagellate and copepod layers*	-66%	not applicable	-81%
<i>x</i>	60 cm	not applicable	not applicable	-28%
<i>d</i>	3 µm	+1.8%	0%	0%
	7 µm	-0.8%	0%	0%
Δt	0.016 s	-36%	-22%	-38%
	1.6 s	+40%	+24%	+40%
<i>q</i>	0.05	-31%	-19%	-35%
<i>X</i>	1·10 ⁻³	0%	0%	-7%
<i>M</i>	3.00	+0.2%	0%	0%

*The lower intensity of dinoflagellate and copepod bioluminescent flashes is often compensated by much higher densities than those typical of bioluminescent gelatinous zooplankton [14, S9].

Supplemental References

- S1. Snyder, A.W. (1975). Photoreceptor optics - Theoretical principles. In Photoreceptor optics, A.W. Snyder and R. Menzel eds. (Berlin, Heidelberg, New York: Springer), pp. 38-55.
- S2. Warrant, E.J. (2000). The eyes of deep-sea fishes and the changing nature of visual scenes with depth. *Phil. Trans. R. Soc. Lond. B.* 355, 1155-1159.
- S3. Johnsen, S. (2002). Cryptic and conspicuous coloration in the pelagic environment. *Proc. R. Soc. Lond. B.* 269, 243-256.
- S4. Clark, P.J. and Evans, F.C. (1954). Distance to Nearest Neighbor as a Measure of Spatial Relationships in Populations. *Ecology* 35, 445-453.
- S5. Govardovskii, V.I., Fyhrquist, N., Reuter, T., Kuzmin, D.G. and Donner, K. (2000). In search of the visual pigment template. *Visual Neurosci.* 17, 509-528.
- S6. Watkins, W.A., Daher, M.A., Dimarzio, N.A., Samuel, A., Wartzok, D., Fristrup, K.M., Howey, P.W. and Maiefs, R.R. (2002). Sperm whale dives tracked by radio telemetry. *Mar. Mammal Sci.* 18, 55-68.
- S7. Watwood, S.L., Miller, P.J.O., Johnson, M., Madsen, P.T. and Tyack, P.L. (2006). Deep-diving foraging behaviour of sperm whales (*Physeter macrocephalus*). *J. Animal Ecol.* 75, 814-825.
- S8. Landman, N.H., Cochran, J.K., Cerrato, R., Mak, J., Roper, C.F.E. and Lu, C.C. (2004). Habitat and age of the giant squid (*Architeuthis sanctipauli*) inferred from isotopic analyses. *Mar. Biol.* 144, 685-691.
- S9. Nicol, J.A.C. (1971). Physiological investigations of oceanic animals. In Deep oceans, P.J. Herring and M.R. Clarke eds. (London: Arthur Barker), pp. 225-246.
- S10. Moeller, J.F. and Case, J.F. (1994). Properties of visual interneurons in a deep-sea mysid, *Gnathophausia ingens*. *Mar. Biol.* 119, 211-219.
- S11. Moeller, J.F. and Case, J.F. (1995). Temporal adaptations in visual systems of deep-sea crustaceans. *Mar. Biol.* 123, 47-54.
- S12. 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.
- S13. Matthiessen, L. (1882). Über die Beziehung, welche zwischen dem Brechungsindex des Kemcentrums der Krystalllinse und dem Dimension des Auges bestehen. *Pflügers Arch.* 27, 510-523.

An interplay between short- and long-range interactions is a crucial element in a mathematical model of biological pattern formation formulated by Alan Turing in 1952 [11,12]. Turing, whose 100th anniversary was commemorated earlier this year, formulated this mathematical model based on concentrations of two substances, an activator and an inhibitor. The activator activates its own synthesis and that of an inhibitor, which inhibits the activator, and both substances diffuse away from the source at different rates. Depending on which parameters are chosen, a regular periodic pattern of substance distribution can emerge. What is exciting about this model is that the pattern can basically arise from ‘nothing’, i.e. from very small fluctuations of initial concentrations. In that sense, it is appealing to think of the zebrafish stripes, which also have self-organising characteristics, as Turing patterns.

Turing conceived his model as a purely mathematical system in one dimension, but simulations based on Turing models can give rise to an amazing variety of biological patterns, from sea shells to cats [12]. Such a general model is naturally appealing for biologists who often lament the lack of unified theories in their field, but the challenge is to identify how it is implemented in the real world. Obviously, Turing could not know about the principles and intricacies of cellular signalling. So, in the study of real-life Turing patterns, the abstract roles of his ‘activator’ and inhibitor’

need to be played by real molecules or cells. One of the most clear-cut incarnations of a Turing mechanism in the context of a periodic pattern was found in the spacing of hair follicles in mice, where the signalling molecule WNT is acting as an activator and its antagonist DKK as the inhibitor [13].

Sure enough, Turing patterns can also match with astonishing precision the colour patterns observed in zebrafish under various conditions [10]. However, it is not yet clear whether such an activator–inhibitor system is really at play here, and if so how it is implemented. It need not be as literal as in the case of mouse hair follicle spacing. Instead, the ‘activator’ could be a stimulation of proliferation, and the inhibitor could be the repulsion seen when melanophores and xanthophores bump into each other. Integrating the electrical properties of the pigment cells into a Turing model will be a challenge. But the idea that the stripes of zebrafish could be a Turing pattern come to life organised by membrane potentials — something rarely considered in the context of developmental pattern formation — is definitely an electrifying one.

References

1. Parichy, D.M. (2003). Pigment patterns: fish in stripes and spots. *Curr. Biol.* 12, R947–R950.
2. Inaba, M., Yamanaka, H., and Kondo, S. (2012). Pigment pattern formation by contact-dependent depolarization. *Science* 335, 677.
3. Yamaguchi, M., Yoshimoto, E., and Kondo, S. (2007). Pattern regulation in the stripe of zebrafish suggests an underlying dynamic and autonomous mechanism. *Proc. Natl. Acad. Sci. USA* 104, 4790–4793.
4. Parchem, R.J., Perry, M.W., and Patel, N.H. (2007). Patterns on the insect wing. *Curr. Opin. Genet. Dev.* 17, 300–308.
5. van Eeden, F.J., Granato, M., Schach, U., Brand, M., Furutani-Seiki, M., Haffter, P., Hammerschmidt, M., Heisenberg, C.P., Jiang, Y.J., Kane, D.A., et al. (1996). Genetic analysis of fin formation in the zebrafish, *Danio rerio*. *Development* 123, 255–262.
6. Haffter, P., Odenthal, J., Mullins, M.C., Lin, S., Farrell, M.J., Vogelsang, E., and Nüsslein-Volhard, C. (1996). Mutations affecting pigmentation and shape of the adult zebrafish. *Dev. Genes Evol.* 206, 260–276.
7. Maderspacher, F., and Nüsslein-Volhard, C. (2003). Formation of the adult pigment pattern in zebrafish requires leopard and obelix dependent cell interactions. *Development* 130, 3447–3457.
8. Watanabe, M., Iwashita, M., Ishii, M., Kurachi, Y., Kawakami, A., Kondo, S., and Okada, N. (2006). Spot pattern of leopard *Danio* is caused by mutation in the zebrafish connexin 41.8 gene. *EMBO Rep.* 7, 893–897.
9. Iwashita, M., Watanabe, M., Ishii, M., Chen, T., Johnson, S.L., Kurachi, Y., Okada, N., and Kondo, S. (2006). Pigment pattern in jaguar/obelix zebrafish is caused by a Kir7.1 mutation: implications for the regulation of melanosome movement. *PLoS Genet.* 2, e197.
10. Nakamasu, A., Takahashi, G., Kanbe, A., and Kondo, S. (2009). Interactions between zebrafish pigment cells responsible for the generation of Turing patterns. *Proc. Natl. Acad. Sci. USA* 106, 8429–8434.
11. Turing, A.M. (1952). The chemical basis of morphogenesis. *Phil. Transact. Roy. Soc. London B* 237, 37–72.
12. Kondo, S., and Miura, T. (2010). Reaction-diffusion model as a framework for understanding biological pattern formation. *Science* 329, 1616–1620.
13. Sick, S., Reinker, S., Timmer, J., and Schlake, T. (2006). WNT and DKK determine hair follicle spacing through a reaction-diffusion mechanism. *Science* 314, 1447–1450.

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Sensory Ecology: Giant Eyes for Giant Predators?

Mathematical models suggest the enormous eyes of giant and colossal squid evolved to see the bioluminescence induced by the approach of predatory whales.

Julian C. Partridge

In the American Museum of Natural History, a striking diorama (Figure 1) depicts a battle between one of the world's largest mammals and its second largest invertebrate: in the darkness of a deep ocean, a sperm whale wrestles a giant squid. Although

this interaction has never been witnessed, these species have captured the human imagination for millennia, and their putative combat for centuries. In stories and myth sperm whales (*Physeter macrocephalus*) and giant squid (*Architeuthis* spp.) are conjured as terrible and terrifying animals, easily provoked to attack both

seafarers and their ships. Such attacks on ships may have occurred, but attacks by whales on squid are certainly much more common: giant squid are undoubtedly important components of the diet of sperm whales, squid beaks often being found in sperm whale guts, and the skin of sperm whales often bearing scars from giant squids' formidable suckers. Indeed, predation of giant squid by sperm whales can be considered the culmination of an approximately 30 million year evolutionary arms race between cephalopods and whales. This race is marked by an interesting sensory imbalance, in which whales depend on reflected sound to find

their prey, but the squid, in arguments developed by Nilsson and colleagues [1] in this issue of *Current Biology*, rely mainly on vision to detect their predators. Moreover, this new work suggests that the extraordinarily large eyes of the giant squid, and the related colossal squid *Mesonychoteuthis* sp., have evolved *specifically* to see large predators.

Like vertebrates, squid eyes are ‘simple’ or ‘camera-type’, in which a single lens forms an image on the photoreceptor layer of the retina, but giant and colossal squid do indeed have giant eyes. Human eyes, for comparison, are roughly 24 mm in diameter and those of horses or cows are about 34 mm, whilst ostriches (the terrestrial animal with the largest eyes) have eyes some 50 mm in diameter. Sperm whales have similar sized eyes to those of ostriches (55 mm) and blue whales, the world’s biggest vertebrate, have eyes some 150 mm in diameter, though up to a third of that is taken up with a very thick sclera, and internal dimensions are less and thus they, and other giants of the sea such as swordfish, effectively have comparably sized eyes, some 90 mm in diameter. In contrast, the eyes of *Architeuthis* and *Mesonychoteuthis* are huge, up to 270 mm in diameter and bigger than a soccer ball, begging the question: ‘why?’

The answer is likely to lie in the optical biophysics of their eyes and, just as importantly, what they have evolved to see. In general, big eyes provide both higher sensitivity and higher spatial resolution. Temporal resolution (the ‘shutter speed’ of an eye) aside, sensitivity and resolution are the main variables underpinning ocular anatomy: big eyes perform better; the counteracting costs being metabolic expense and physical bulk. In the deep sea, which is essentially dark and where animals occur in very low densities, sensitive eyes confer an important advantage as they allow their owners to see smaller objects further away, and therefore visually to survey a greater volume of their surrounds. Sensitivity is, however, highly dependent on visual task [2–4]. For broad sources of light, with which we are most familiar in our environment, retinal irradiance, and hence sensitivity is determined by the f-number: the ratio of the focal length (f) to the lens diameter. For this reason the small eyes of mice (f -number = $f/0.9$)



Figure 1. Battle of the giants.

Life sized models of *Physeter* and *Architeuthis* battle it out in the famous ‘Squid and Whale’ diorama of the American Museum of Natural History’s Milstein Hall of Ocean Life (credit: AMNH/D. Finnin).

are much more sensitive than ours (f -number = $f/2$ in darkness with open pupil), and provide them with a retinal image some five times brighter [5]. For the visualisation of point sources, such as stars, however, it is pupil diameter that counts — which is why the best telescopes tend to have the largest mirrors or lenses. Viewing stars is obviously not a visual task of relevance in the deep sea, but point sources of light are common, in the form of bioluminescence, and the ability to see bioluminescence may be exactly what giant squid depend on to see approaching whales. What is unusual, argue Nilsson and colleagues [1], is it is not individual point sources that the giant squid need to visualize, but rather the combined light from many such sources flashing in unison.

Spontaneous bioluminescence in the deep sea is remarkably uncommon, but bioluminescent animals (and some 90% of deep sea animals have the ability) are easily induced to flash when disturbed [6], a fact no doubt well appreciated by naval submariners. For this reason, it might be considered advantageous for deep-sea predators to adopt a sit-and-wait strategy and many, including giant squid, may well do so. For the highly energetic mammalian whales, however, this is not an option, as food is too widely dispersed and too rarely encountered in the mesopelagic to do without active

searching. What little we know of sperm whale foraging suggests that they descend at about 1.5 ms^{-1} [7] before actively searching, and some studies [8] suggest they intersperse steady 2 ms^{-1} swimming with bursts of speed, including sprints up to 9 ms^{-1} (32 kph). Such swimming speeds are similar to those of other cetacean-hunting toothed whales [9] and will undoubtedly trigger bioluminescence: dolphins swimming at much lower speeds through seas rich in bioluminescent organisms glow brightly (Figure 2), revealing striking detail about their body form [10]. Even in relatively impoverished mesopelagic water, foraging sperm whales may thus be similarly illuminated, particularly if giant squid favour zones with higher biomass and hence more potential bioluminescence.

What Nilsson and colleagues [1] have done is to calculate how the size of an eye is optimised for different visual tasks and, having taken into consideration a raft of variables about the emission and transmission of light underwater, eye geometry, visual optics, photoreceptor properties, and so on, they conclude that giant and colossal squids’ eyes have evolved for a purpose not shared by other animals: the detection of form illumination due to bioluminescence induced by foraging whales. Their models show that, in shallow water, objects are most easily detected as dark silhouettes

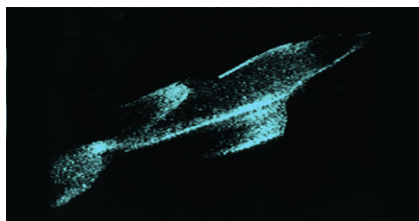


Figure 2. Revealed by bioluminescence.

Bioluminescence induced by a 2.7 m long Atlantic bottle-nosed dolphin (*Tursiops truncatus*) gliding at $\sim 0.1 \text{ ms}^{-1}$ in San Diego Bay and filmed with an intensified video camera. (Photograph from Michael Latz, Scripps Institution of Oceanography, University of California San Diego.)

seen against the brighter down-welling space light but, under most conditions, the detection of bright point sources provides the longest visual range. For these tasks, eyes no bigger than 90 mm in diameter are needed, and returns diminish rapidly for larger eyes. The only notable feature that sets very large eyes apart is that they are superior for detecting big, low contrast, luminous objects at long visualisation ranges and depths where daylight is insignificant. Thus, counter-intuitively, the authors suggest that the huge eyes of giant and colossal squid have evolved for a particular low-resolution visual task: to spot large, dimly glowing, approaching whales.

The evolution of the toothed whales has long been intimately associated with hunting cephalopods [11] and today squid and octopus feature in the diets of 90% of toothed whales: perhaps unsurprising as oceanic cephalopods are a massive food resource. Rising in the early Oligocene some 34 million years ago, the earliest echolocating toothed whales were relatively late arrivals in the evolutionary history of squid. The ancient cephalopods arose in the Cambrian, but squid are evolutionary upstarts, evolving 'only' some 150 millions years ago. Vision may have been important for the first whales, but sonar soon evolved, perhaps to help hunting in shallow seas at night, and perhaps because cephalopods are essentially deaf to whales' sonar. Squids do not hear the clicks and creaks of whale echolocation, the sonar frequencies being beyond their sensitivity spectrum despite the intense sounds whales produce [12,13]. Squids are poor acoustic targets, lacking gas filled swim

bladders or dense skeletal elements to reflect sound, although their muscular arms and mantle, and chitinous beak will produce some echo. The first echolocating toothed whales may have eaten solid-shelled nautiloids that would have been easy to detect with sound, but detecting softer-bodied squids is harder. In consequence, sperm whales make one of the loudest noises in the animal kingdom and are calculated to be able to detect 250 mm *Loligo* squid up to 325 m away, and muscular 1.5 m long Humboldt squid (*Dosidicus gigas*) at as far as 1000 m [12–14]. No doubt relatively flaccid mesopelagic squid, giant squid included, are more acoustically cryptic and so difficult to detect, but it is likely that these are detectable beyond 100 m. Neatly, this is about the distance at which giant squid might see approaching whales calculated by Nilsson and colleagues [1].

Where behaviour is difficult or impossible to observe, modelling visual performance is one way to gain insights about how animals may interact, and to identify selective pressures that might be operating on their evolution. In the context of giant squid the mathematical models of Nilsson and colleagues [1] suggest why they may have such giant eyes, although, much as it is fascinating to speculate, significant caveats inevitably remain. For instance, although giant squid have eyes much larger than those of similar sized, or larger, fish and whales, they may not actually be out of proportion compared with those of other cephalopods. At this point, the allometric scaling of eye size with body size, such as has been undertaken for many taxa of vertebrates [15], remains unresolved for squid but, as always in comparative biology, phylogeny needs to be considered; even when physics appears to dominate an argument. The extinct ichthyosaurs, giant marine reptiles that lived 250–90 million years ago, had eyes at least as big as those of giant squid, for similar body sizes [16], and a cursory examination suggests squid eye sizes may fit within the confidence limits of ichthyosaur eye size allometry. Did ichthyosaurs too need to detect large glowing predators? Despite the efforts of both scientists and filmmakers, we know too little about the way in which sperm whales catch giant squid and,

until we have direct observations, intriguing mathematical models and imaginative dioramas may be the best we have.

References

1. Nilsson, D.-E., Warrant, E.J., Johnsen, S., Hanlon, R., and Shashar, N. (2012). A unique advantage for giant eyes in giant squid. *Curr. Biol.* 22, 683–688.
2. 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.
3. Warrant, E.J., and Lockett, N.A. (2004). Vision in the deep sea. *Biol. Rev.* 79, 671–712.
4. Warrant, E.J. (2004). Vision in the dimmest habitats on earth. *J. Comp. Physiol. A* 190, 765–789.
5. Land, M.F., and Nilsson, D.-E. (2002). *Animal Eyes* (Oxford, New York: Oxford University Press).
6. Widder, E.A. (2001). Bioluminescence and the pelagic visual environment. *Mar. Freshw. Behav. Physiol.* 35, 1–26.
7. Miller, P.J.O., Johnson, M.P., Tyack, P.L., and Terray, E.A. (2004). Swimming gaits, passive drag and buoyancy of diving sperm whales *Physeter macrocephalus*. *J. Exp. Biol.* 207, 1953–1967.
8. Aoki, K., Amano, M., Sugiyama, N., Muramoto, H., Suzuki, M., Yoshioka, M., Mori, K., Tokuda, D., and Miyazaki, N. (2007). Measurement of swimming speed in sperm whales. Symposium on Underwater Technology and Workshop on Scientific Submarine Cables and Related Technologies 2007. pp. 467–471.
9. Soto, N.A., Johnson, M.P., Madsen, P.T., Diaz, F., Dominguez, I., Brito, A., and Tyack, P. (2008). Cheetahs of the deep sea: deep foraging sprints in short-finned pilot whales off Tenerife (Canary Islands). *J. Anim. Ecol.* 77, 936–947.
10. Rohr, J., Latz, M.I., Fallon, S., Nauen, J.C., and Hendricks, E. (1998). Experimental approaches towards intercepting dolphin stimulated bioluminescence. *J. Exp. Biol.* 201, 1447–1460.
11. Lindberg, D.R., and Pyenson, N.D. (2007). Things that go bump in the night: evolutionary interactions between cephalopods and cetaceans in the tertiary. *Lethaia* 40, 335–343.
12. Madsen, P.T., Wilson, M., Johnson, M., Hanlon, R.T., Bocconcelli, A., Aguilar Soto, N., and Tyack, P.T. (2007). Clicking for calamari: toothed whales can echolocate squid *Loligo pealeii*. *Aquatic Biol.* 1, 141–150.
13. Wilson, M., Hanlon, R.T., Tyack, P.L., and Madsen, P.T. (2007). Intense ultrasonic clicks from echo locating toothed whales do not elicit anti-predator responses or debilitate the squid *Loligo pealeii*. *Biol. Lett.* 3, 225–227.
14. André, M., Johansson, T., Delory, E., and van der Schaar, M. (2007). Foraging on squid: the sperm whale mid-range sonar. *J. Mar. Biol. Ass. UK* 87, 59–67.
15. Howland, H.C., Merola, S., and Basarab, J.R. (2004). The allometry and scaling of the size of vertebrate eyes. *Vis. Res.* 44, 2043–2065.
16. Montani, R., Rothschild, B.M., and Wahl, W. (1999). Large eyeballs in diving ichthyosaurs. *Nature* 402, 747.

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