

The eyes of deep-sea fishes and the changing nature of visual scenes with depth

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The visual scenes viewed by ocean animals change dramatically with depth. In the brighter epipelagic depths, daylight provides an extended field of illumination. In mesopelagic depths down to 1000 m the visual scene is semi-extended, with the downwelling daylight providing increasingly dim extended illumination with depth. In contrast, greater depths increase the prominence of point-source bioluminescent flashes. In bathypelagic depths (below 1000 m) daylight no longer penetrates, and the visual scene consists exclusively of point-source bioluminescent flashes. In this paper, I show that the eyes of fishes match this change from extended to point-source illumination, becoming increasingly foveate and spatially acute with increasing depth. A sharp fovea is optimal for localizing point sources. Quite contrary to their reputation as 'degenerate' and 'regressed', I show here that the remarkably prominent foveae and relatively large pupils of bathypelagic fishes give them excellent perception and localization of bioluminescent flashes up to a few tens of metres distant. In a world with almost no food, where fishes are weak and must swim very slowly, this range of detection (and interception) is energetically realistic, with distances greater than this physically beyond range. Larger and more sensitive eyes would give bathypelagic fishes little more than the useless ability to see flashes beyond reach.

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1. INTRODUCTION

'The bathypelagic zone, the largest environment on earth, is cold and dark (apart from fitful sparks of living light) and the most deserted life zone in the ocean, both in numbers of organisms and of species.' So begins Norman Marshall's description of life and nutrition at depths below 1000 m, from his 1979 classic *Developments in deep-sea biology* (p. 253). Marshall paints an eerie picture of a dark world with little food, where most animals have been forced to adopt incredibly low respiration rates to survive. With food a rarity, the muscles of most bathypelagic fishes and crustaceans have become watery and weak, their skeletons flimsy and their internal organs diminished. Consequently, compared to their relatives from brighter shallower waters, bathypelagic deep-sea fishes (as seen from the windows of submersibles) generally move very slowly. Their eyes appear to follow the same pattern, frequently being described as 'small', 'regressed' or 'degenerate', no doubt casualties of the unsustainable energy cost of supporting large eyes (Laughlin *et al.* 1998). Marshall's 'fitful sparks' of bioluminescence—rare and dim—are the only things they see. But not seeing them reliably could have serious consequences. Failing to see a bioluminescent flash could mean missing a rare meal, or losing a seldom-encountered mate. Far from being 'degenerate', the eyes of bathypelagic fishes should actually be of utmost importance. A survey of recent work suggests that they are important, with many having frontally directed foveae of high anatomical acuity (Wagner *et al.* 1998). As I show here, these foveae, and disproportionately large pupils, provide the eyes of bathypelagic fishes with sufficient sensitivity and

resolution to locate bioluminescent flashes accurately at ecologically meaningful distances. Rather than being degenerate, the eyes of bathypelagic fishes are perfectly adequate for life in a dark, slow-motion world pierced by pinpoints of light.

2. VISUAL SCENES AND EYE DESIGN IN THE OCEAN

In the clearest oceans, light becomes dimmer and bluer with increasing depth, and increasingly incident from above. For every 100 m of depth, light intensity is reduced by 1.5 orders of magnitude. To put this figure in perspective, during the day at 700 m there would be insufficient daylight to sustain human vision. Below 1000 m almost no daylight remains, certainly not enough to be seen by deep-sea animals (Denton 1990). At these depths, the only visible lights are point-source bioluminescent signals produced by other animals (although in some cases these signals can be somewhat larger than point sources, as in the tunicate *Pyrosoma*). Bioluminescent signals are often flashes, whose length may vary from hundreds of milliseconds to several seconds, and whose frequency in the sea can vary between one and 160 flashes from each steradian of water per minute. Below 1000 m, flash frequency drops considerably and becomes very infrequent below 2000 m (Clarke & Hubbard 1959). The intensity and colour of these flashes can be quite variable (see Herring 1978), but a typical flash is blue in colour and contains between 10^7 and 10^{13} photons, no doubt a highly visible stimulus in the darkness of the deep sea. During the day in the brighter depths above 100 m, bioluminescent flashes are not visible (Denton 1990).

We have now touched on a topic that is of crucial importance to the design of oceanic eyes, and the key to understanding why those of bathypelagic fishes are formed the way they are: the nature of visual scenes changes with depth. In shallower depths, where daylight is scattered to produce an even blue space light and where the sea floor may be clearly visible, the visual scenes viewed by animals are extended in all directions. But at greater depths, where the space light is diminished, bioluminescent point sources also begin to appear, especially from below where the space light is up to 1000 times dimmer than that coming from above. Upwards, and even frontwards (where the space light is only ten times dimmer), the scene is still extended. But downwards the scene begins to be dominated by point sources. At still deeper levels, bioluminescent point sources can be seen in all directions. In these mesopelagic depths (150–1000 m) the scene can be nebulously referred to as semi-extended, becoming less and less extended and more and more point-like as the space light diminishes with increasing depth. Below 1000 m, where daylight no longer penetrates, the visual scene is entirely point-like in nature.

How should an eye be optimally designed to view a particular visual scene? To detect an increasingly dim extended field of space light (and all objects illuminated by it) eyes need to be bigger, with larger pupils (Land 1990). The visual channels—defined by the array of retinal ganglion cells (Collin 1997)—need to sample photons over longer integration times (temporal summation) from wider, and thus more sensitive, receptive fields (spatial summation) (Warrant 1999). Mesopelagic eyes constructed to view dim extended scenes should have ganglion cells with wide receptive fields derived from large numbers of photoreceptors.

A quite different eye design is predicted for the point-source world of the bathypelagic zone. A large pupil will still be necessary for catching as much light as possible from point sources. Spatial summation, however, is now quite a useless strategy. The image of the point source formed on the retina, like the point source itself, will be small, its size determined only by the severity of aberration and diffraction in the lens, neither of which are severe in fishes. For a ganglion cell to catch all the light from this image, its receptive field need not be any larger than the image itself. Nothing would be gained from further summation using larger pools of photoreceptors as such a strategy makes sense only for an extended source (Warrant 1999). Eyes viewing point sources should thus tend towards high anatomical acuity, although there is one possible exception: some deep-sea fishes can illuminate their surroundings with in-built bioluminescent headlamps, and these fishes may very well view extended scenes. The point-source arguments just elaborated would then not apply and, depending on the intensity of the illumination, the retinas of such fishes may look more like those of their mesopelagic cousins.

The gradual change from an extended to a point source world does in fact bring with it the predicted changes in eye design. Down to the limits of daylight, the eyes of fishes generally increase in size relative to body length and their pupils enlarge. The enormous tubular eyes of fishes from the lower mesopelagic depths are an excellent

example. But this trend ceases upon transition to the bathypelagic zone. Here fishes are forced to have smaller eyes, their food supplies and respiration rates incapable of supplying the energy needed to support larger eyes. However, compared with eye size, their pupils are larger than those of their relatives from the daylight zone. As I show in §3, these pupils are quite adequate for catching reliable photon samples from bioluminescent flashes in the deep.

Do the predicted changes in retinal spatial summation also occur with increasing depth? The answer to this question can be found in the recent impressive work of Wagner and colleagues (1998) who surveyed the eyes and retinas of a large number of fishes living at known depths. From their data, it is possible to plot the angular separation of ganglion cells as a function of depth for some 20 species of deep-sea fishes. A narrower separation of ganglion cells results in a greater anatomical acuity. The results (figure 1a) show two important features. First, the eyes of fishes, on average, actually become sharper with depth, even in the mesopelagic, which at first seems like a contradiction. However, as predicted, the eyes of bathypelagic fishes are the sharpest, typically having the potential to resolve details subtending just 5 arcmin. This implies that the ganglion cells of bathypelagic fishes are tightly organized into well-developed foveae and areae centrales, with each ganglion cell receiving input from a small pool of photoreceptors. The sharp frontally directed fovea of *Rouleina attrita* (figure 1b)—a fish living between 1.4 and 2.1 km below the sea surface—is an excellent example (Wagner *et al.* 1998).

Second—and this explains the contradiction—the variation across species in ganglion cell separation (and thus acuity) is large in the brighter upper levels (figure 1a, error bars), but gradually declines with depth, with minimal variation in the bathypelagic zone (separation = 4.8 ± 2.9 arcmin). The small variation in the bathypelagic is easy to understand: here the only light sources are point sources and the only sensible strategy involves little summation and high acuity. This is also the key to understanding the variation at mesopelagic depths, the realm of semi-extended scenes. Some fishes have eyes adapted for seeing extended objects illuminated by the dim downwelling daylight, and these should therefore display greater spatial summation—and poorer acuity—with depth (Warrant 1999), as indeed seems to be the case (Wagner *et al.* 1998). Other mesopelagic fishes have a lifestyle dependent on the detection of bioluminescent point sources and should thus tend towards greater acuity. Yet other fishes have eyes adapted for both types of sources—indeed, deep-sea scotelarchids (*Scopelarchus* sp.) seem to have retinal areas devoted separately to point sources and extended sources (see Wagner *et al.* 1998). The semi-extended nature of the mesopelagic depths may well explain the frustration felt by Murray and Hjort when, in 1912, they wrote ‘Nothing seems more hopeless in biological oceanography than the attempt to explain the connection between the development of the eyes and the intensity of light at different depths in the ocean’ (as quoted by Denton 1990, p. 127). The intensity of light is not in itself the overriding influence on eye design but rather its organization into extended or point-like features.

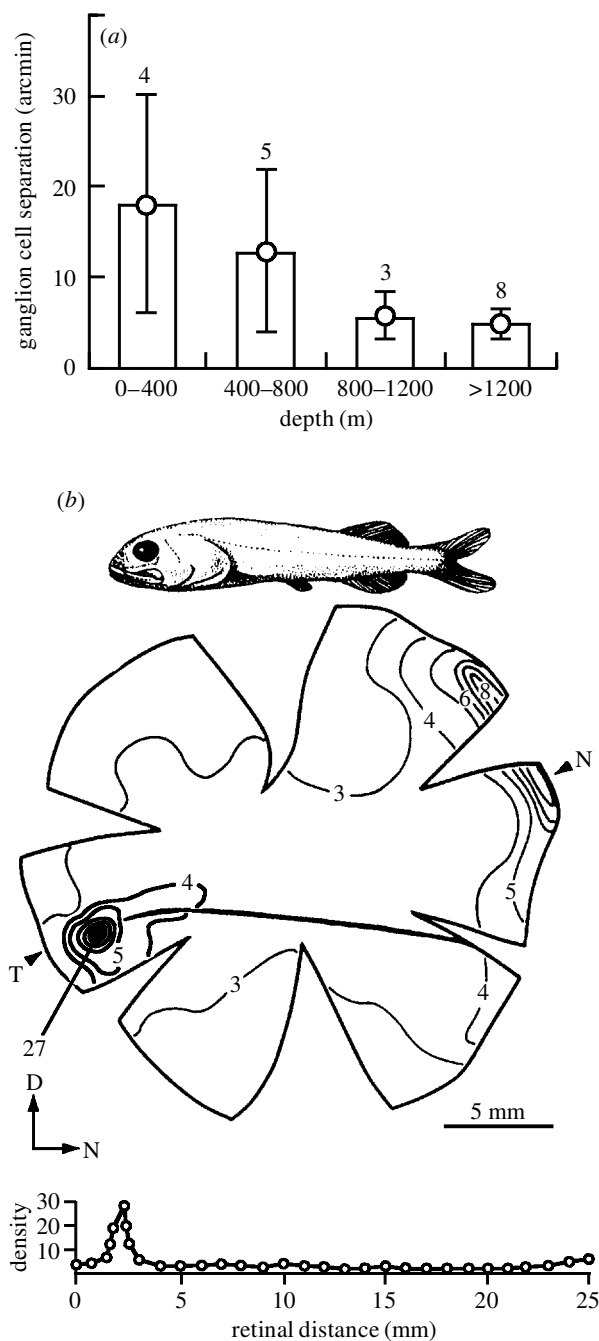


Figure 1. Anatomical acuity and habitat depth in deep-sea fishes. (a) The angular separation of ganglion cells (in arcmin)—from which anatomical acuity is derived—is shown as a function of depth in 20 species of deep-sea fishes (data assembled from tables given in Wagner *et al.* (1998), with number of included species indicated above each histogram bar). A narrower separation of ganglion cells results in a greater anatomical acuity. Average cell separation becomes narrower with increasing depth, implying that anatomical acuity becomes sharper. Cell separation (and thus acuity) also becomes less variable (error bars indicate total spread). (b) The sharp temporal (forward-pointing) fovea of the bathypelagic fish *Rouleina attrita*, a fish living at depths between 1400 and 2100 m (upper diagram). The middle diagram shows a retinal whole mount, with numbered cell density contours representing cell density isolines in the ganglion cell layer ($\times 10^3 \text{ cells mm}^{-2}$). Cell density rises rapidly in the temporal fovea ($27 \times 10^3 \text{ cells mm}^{-2}$), as does anatomical acuity (4.7 arcmin at the foveal centre). A shallower rise in

3. HOW WELL DO BATHYPELAGIC FISHES SEE BIOLUMINESCENT FLASHES?

Just how 'degenerate' are the eyes of bathypelagic fishes? Does their smaller size—the product of an impoverished environment—actually hinder perception of bioluminescent flashes? Exactly how well a bathypelagic fish can detect and localize bioluminescent flashes will depend on the sensitivity of its eye, the intensity and distance of the flash and the attenuating effects of water.

The intensity of typical bioluminescent flashes varies between 10^{-11} and 10^{-7} W m^{-2} at a distance of 1 m (Nicol 1971). If we assume these bioluminescent point sources are blue ($\lambda = 475 \text{ nm}$) and radiate in all directions through a sphere of radius 1 m (M. F. Land, personal communication), then at source these flashes will emit between 3×10^8 and 3×10^{12} photons every second. Because flashes are typically between 0.2 and 5 s long (Clarke & Hubbard 1959), the total number of photons E contained within a flash will vary between the extremes of a dim short flash (6×10^7 photons) and a bright long flash (2×10^{13} photons).

How many photons N from a bioluminescent flash containing E photons enter the eye of a fish of pupil diameter A at a distance r from the flash? It is easy to show (see Appendix A) that the number of photons N is given in equation (1).

$$N = \frac{EA^2}{16r^2} e^{-\alpha r}. \quad (1)$$

The exponential term describes the attenuation of the bioluminescent flash due to the scattering and absorption of light by water, and α is the total attenuation coefficient (Lythgoe 1979). For clear water and blue light, $\alpha = 0.05 \text{ m}^{-1}$ (Denton 1990).

According to Denton (1990), a deep-sea fish needs to sample about five photons to allow threshold perception of a blue bioluminescent flash. Thus, if we set $N = 5$ photons, and assume that deep-sea fishes have long integration times (as one would predict from theory, see Warrant (1999)), we can now ask the following important question: How far away can a fish with a certain pupil size perceive a bioluminescent flash of a given intensity? First we need to know how large bathypelagic pupils actually are. Data from eight bathypelagic fishes (in Wagner *et al.* 1998) give an average pupil diameter of $7.3 \pm 3.7 \text{ mm}$. Consider this average diameter and a flash intensity of 10^{10} photons (also an average bathypelagic value). With $N = 5$ photons and $\alpha = 0.05 \text{ m}^{-1}$, it is possible to solve equation (1) numerically to obtain $r = 34 \text{ m}$. In other words, a fish with a 7.3-mm-wide pupil will see this flash at distances up to 34 m away. Such distances are plotted for different flash intensities and pupil diameters in figure 2. Brighter flashes can be seen further away, but even for the brightest flashes and the largest pupils the maximum range of visibility is about 150 m.

cell density is also seen nasally. The graph shows cell density ($\times 10^3 \text{ cells mm}^{-2}$) plotted along a temporal–nasal transect (between the arrowheads shown on the whole mount) and clearly reveals the fovea. D, dorsal; N, nasal; T, temporal. Diagram modified from Wagner *et al.* (1998).

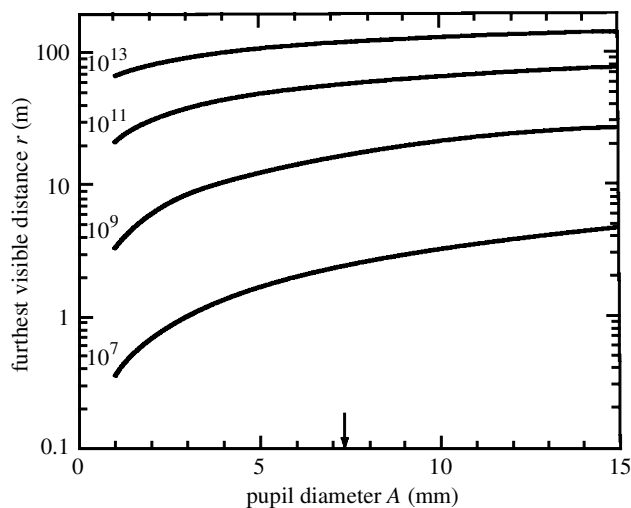


Figure 2. The visibility of bioluminescent point sources in bathypelagic fishes. The farthest distance r (m) that a fish with pupil diameter A (mm) can see a bioluminescent flash containing E photons was calculated numerically from equation (1) (for threshold detection ($N = 5$ photons) and attenuation coefficient $\alpha = 0.05 \text{ m}^{-1}$). Curves are shown for different flash intensities (E), ranging from the dimmest (10^7 photons) to the brightest (10^{13} photons) measured in the ocean. Brighter flashes or larger pupils extend the range of visibility, although beyond 150 m flashes are not likely to be visible. For typical pupils and flash intensities (around 7.3 mm diameter (arrow) and 10^{10} photons, respectively), the range is about 30–40 m.

The eyes of bathypelagic fishes are therefore quite adequate for seeing bioluminescent flashes up to several tens of metres away. At first glance this range does not seem particularly great. But for a bathypelagic fish, with watery muscles and a weakly ossified skeleton, distances of tens of metres are very great indeed. It is not likely that these fishes are capable of top speeds much greater than about one body length per second (Marshall 1979), which means that a fish of 10 cm length would require about 10 min to reach a flash produced 60 m away. During a 10 min interception, the producer of the flash might have moved an impossibly large distance away. The fish, having expended a tremendous amount of precious energy, would probably have little chance of finding its potential mate or prey (unless flash production is quite frequent). In general it is more likely that detection and interception takes place over much smaller distances, and for this task the sensitivity of their eyes is more than adequate. Having eyes any larger or more sensitive would do little more than allow them to see flashes beyond reach. And with energy at such a premium, larger eyes requiring much greater energy expenditure (Laughlin *et al.* 1998) would not be a viable option anyway.

Finally, we turn to the resolution of bathypelagic eyes. How well are the small receptive fields of the ganglion cells matched to the size of the point-source bioluminescent images produced on the retina? If we assume for the moment that aberrations are negligible, the size of the point-source image will be determined only by the diffraction of light entering the pupil. The width of this image, as set by the width of the diffraction Airy disc, is given by the Rayleigh criterion— $2.44 \lambda / A$ radians—where λ is the wavelength of light (e.g. 475 nm) and A is

the pupil diameter. If we assume $A = 7.3$ mm, the width of the image is about 0.5 arcmin, which is ten times smaller than the receptive fields of foveal ganglion cells (ca. 5 arcmin; figure 1a). After adding the inevitable (but minor) lens aberrations, image size is probably rather well matched to the receptive field size.

Imagine that a deep-sea fish has detected a flashing bioluminescent source (possibly with its peripheral vision) and has moved to fixate the source frontally. Imagine also that both foveae are pointing forwards into a binocular field of view and that the convergence of the eyes is fixed and independent of eye movements. The sharp resolution afforded by small receptive fields and sharp images would then be a useful aid in determining image disparities in the two eyes, and thereby the distance to the bioluminescent source. A further benefit may also come from the pitted shapes of many bathypelagic foveae. Recent evidence suggests that this shape is ideally suited for estimating the distance of point sources in darkness (Locket 1992). For humans, with an eye separation of 6 cm and foveal ganglion cell receptive fields in the order of 0.5 arcmin, image disparities give reliable distance estimations up to 30 m away. In bathypelagic fishes, with smaller eye separations and larger receptive fields, reliable distance estimation would only be possible at much closer range, maybe only as far away as a few metres. Beyond this range fishes would be unable to distinguish a bright flash impossibly far away from a dim flash nearby. Flash brightness is thus useless for estimating distance and deciding whether a source is worth intercepting. The only useful cue is disparity and its short useful range could act as a filter for ambiguous flashes whose pursuit and attempted interception could expend unacceptably large amounts of precious energy. This is yet another reason why bathypelagic fishes do not need eyes that allow them to see bioluminescent flashes at great distances.

The eyes of bathypelagic fishes, far from being degenerate, are highly adapted for detecting and localizing bioluminescent flashes over ecologically meaningful distances of a few tens of metres. These eyes, together with a battery of other well-developed senses, including the olfactory and lateral line systems, allow bathypelagic fishes the best chance of intercepting mates and prey in a dark, lonely and impoverished world.

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APPENDIX A

Assume light emitted from a bioluminescent point source radiates evenly in all directions. The number of photons N entering a pupil of area $\pi A^2/4$ at a distance r from source depends on the flash intensity at source (E), the light attenuating properties of water ($\propto e^{-\alpha r}$), and the

decline in light flux due to the passage of light through ever larger (imaginary) spherical surfaces (area = $4\pi r^2$). The light flux at distance r is simply given by $E/4\pi r^2$ (Hecht 1987). \mathcal{N} is then just the product of light flux, light attenuation and (circular) pupil area (equation (A1)):

$$\mathcal{N} = \frac{E}{4\pi r^2} \times e^{-\alpha r} \times \frac{\pi}{4} A^2 = \frac{EA^2}{16r^2} e^{-\alpha r}. \quad (\text{A1})$$

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