

Vision in the deep sea

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(Received 2 January 2003; revised 27 November 2003; accepted 1 December 2003)

ABSTRACT

The deep sea is the largest habitat on earth. Its three great faunal environments – the twilight mesopelagic zone, the dark bathypelagic zone and the vast flat expanses of the benthic habitat – are home to a rich fauna of vertebrates and invertebrates. In the mesopelagic zone (150–1000 m), the down-welling daylight creates an extended scene that becomes increasingly dimmer and bluer with depth. The available daylight also originates increasingly from vertically above, and bioluminescent point-source flashes, well contrasted against the dim background daylight, become increasingly visible. In the bathypelagic zone below 1000 m no daylight remains, and the scene becomes entirely dominated by point-like bioluminescence. This changing nature of visual scenes with depth – from extended source to point source – has had a profound effect on the designs of deep-sea eyes, both optically and neurally, a fact that until recently was not fully appreciated. Recent measurements of the sensitivity and spatial resolution of deep-sea eyes – particularly from the camera eyes of fishes and cephalopods and the compound eyes of crustaceans – reveal that ocular designs are well matched to the nature of the visual scene at any given depth. This match between eye design and visual scene is the subject of this review. The greatest variation in eye design is found in the mesopelagic zone, where dim down-welling daylight and bioluminescent point sources may be visible simultaneously. Some mesopelagic eyes rely on spatial and temporal summation to increase sensitivity to a dim extended scene, while others sacrifice this sensitivity to localise pin-points of bright bioluminescence. Yet other eyes have retinal regions separately specialised for each type of light. In the bathypelagic zone, eyes generally get smaller and therefore less sensitive to point sources with increasing depth. In fishes, this insensitivity, combined with surprisingly high spatial resolution, is very well adapted to the detection and localisation of point-source bioluminescence at ecologically meaningful distances. At all depths, the eyes of animals active on and over the nutrient-rich sea floor are generally larger than the eyes of pelagic species. In fishes, the retinal ganglion cells are also frequently arranged in a horizontal visual streak, an adaptation for viewing the wide flat horizon of the sea floor, and all animals living there. These and many other aspects of light and vision in the deep sea are reviewed in support of the following conclusion: it is not only the intensity of light at different depths, but also its distribution in space, which has been a major force in the evolution of deep-sea vision.

Key words: vision, eye design, deep sea, natural scene, visual ecology, bioluminescence, fish, crustacean, cephalopod.

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“Now that he had seen him once, he could picture the fish swimming in the water with his purple pectoral fin set wide as wings and the great erect tail slicing through the dark. I wonder how much he sees at that depth, the old man thought. His eye is huge and a horse, with much less eye, can see in the dark.”

The Old Man and the Sea, Ernest Hemingway

I. INTRODUCTION

The ocean is the largest habitat on earth. Covering nearly three-quarters of the earth's surface and having an average depth of 3800 m (Angel, 1997), the world's oceans contain 1368 million km³ of water and provide a living space 168 times larger than that offered by the airspace and open countryside of terrestrial habitats (Cohen, 1994). Most ocean creatures live in the shallower illuminated depths, although a remarkable variety also live in the vast darkness of the deep (Marshall, 1979). But at all depths the struggle to find food and mates is equally pressing, and vision plays a surprisingly important role.

Daylight only penetrates the upper 1000 m – a small fraction of the ocean's volume – and becomes progressively dimmer and bluer with depth. It is within this ‘photoc zone’ that visual adaptations show the greatest variation. In the vast bathypelagic zone below 1000 m the only light available for vision comes from the bioluminescent flashes produced by marine animals themselves, a stimulus that has largely constrained the types of visual adaptations that have evolved. Until recently, the relationship between eye design and depth was perplexing. In 1912, following collection tours in the North Atlantic aboard the Norwegian steamer *Michael Sars*, Sir John Murray and Johan Hjort exclaimed that ‘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’ (Murray & Hjort, 1912). Recent advances have eased this hopelessness: marine eyes are adapted not only to light intensity *per se*, but also to its spatial organisation. In the ocean, light is organised either as an extended scene of visual features (as in the brighter shallower depths), or is point-like (as is typical of a

bioluminescent flash). Depending on their depth in the ocean, animals can see one or both types of light, with point sources becoming more dominant with increasing depth. Which visual adaptations evolve will depend on which type – point or extended or both – has the greatest ecological meaning, and this of course will vary widely from species to species. Moreover, other more species-specific ecological needs may further influence which adaptations evolve. Thus, at any given depth the spectrum of visual adaptations could be large.

These two dominating influences on the evolution of vision in the deep sea – the changing nature of visual scenes with depth and the natural histories of individual species – form the thematic basis of this review. Following brief descriptions of the marine light environment and how marine eyes are designed, we then explore how eyes have evolved for vision in the three great faunal environments of the deep sea: the mesopelagic zone, the bathypelagic zone and the benthic habitat. It is a story as rich and varied as the deep sea itself.

II. THE FAUNAL ENVIRONMENTS OF THE OCEAN

To understand the evolution of vision in the deep sea one must understand the properties of light in water. Of equal importance is how the biomass of the ocean is distributed with depth. The variety of species and the density of individuals – and consequently the availability of food and mates – is not constant in the ocean. This, as much as light, has been a crucial factor in the evolution of vision, and is the topic to which we turn first.

The ocean's water column and its fauna can be divided into several depth zones. The upper 150–200 m constitute the bright sunlit waters of the epipelagic zone, home to a rich plankton population, large agile predatory fishes (such as tuna, billfishes and sharks) and the smaller varieties of fishes and invertebrates upon which they prey. Epipelagic species are members of a complex phytoplankton-based food web (Lockett, 1977; Marshall, 1979; Gartner, Crabtree & Sulak, 1997) that ultimately supports all life in the ocean via a continuous downward rain of organic material (Angel, 1997). The remainder of the photic zone down to 1000 m constitutes the mesopelagic zone. This region holds the greatest biomass and diversity of animal life found in the ocean, especially in the brighter 'shallow' mesopelagic zone down to about 650 m. It is here – in the twilight zone – that one finds a variety of silvery-sided fishes with dark backs and counter-illuminative light organs, and a rich fauna of transparent and semi-transparent crustaceans, body forms designed for camouflage in the dim down-welling light. It is also here, in this highly competitive world, that some of the most remarkable visual adaptations are found. In the remaining 'deep' mesopelagic zone the biomass and nutrient level drops dramatically. Fishes are dark and non-reflective and crustaceans opaque and red (a good camouflage in the deep sea).

The limit of daylight at 1000 m defines the beginning of the vast bathypelagic zone, the largest and most deserted habitat on earth (Marshall, 1979). This is a dark, still and very cold (1–5 °C) world where food and mates are scarce (Herring, 2000). In one widespread species of anglerfish it has been estimated that less than one female occurs per cubic mile (Pough, Heiser & McFarland, 1996, p. 504)! Bathypelagic animals generally have very low respiration rates, are weak and flimsy, and possess soft skeletons and watery muscles (Marshall, 1979), characteristics that severely limit their locomotive capacities. Below 1000 m, the biomass falls steadily, both in terms of numbers of species and individuals, and then falls exponentially upon entrance to the abyssopelagic subdivision at approximately 2500 m (Marshall, 1979; Angel, 1997). Nutrient levels decline in a similar fashion.

The sea floor, much of it several kilometres below the surface, makes up the wide two-dimensional benthic habitat, whose ooze is the repository of the sparse but continuous rain of organic and inorganic particles known as 'marine snow' (Gartner *et al.*, 1997). Occasionally a large dead animal also sinks to the bottom, providing a veritable food bonanza for benthic organisms, many of which lead a scavenging or filter-feeding lifestyle. Compared to the bathypelagic depths above, the sea floor is rich in nutrients, and home to a variety of animals including bottom-resting fishes, crustaceans, worms, bivalves, sea cucumbers, corals and sponges (Marshall, 1979). The few metres of water directly above the sea floor are the permanent home to many species of crustaceans, squids, and jellyfishes. It is also a temporary home to fishes (such as anglerfishes and lantern fishes) that descend from the pelagic waters above. Several species of benthopelagic fishes – including rat-tails and the often huge deep-sea squaloid sharks – cruise the bottom in search of free-swimming prey (Marshall, 1979; Gartner *et al.*, 1997). Others are benthic (or demersal), such as the scavenging hagfishes which live in burrows dug from the soft silt of the bottom. Benthic and benthopelagic animals tend to be stronger swimmers and physically more robust than their bathypelagic relatives, no doubt the result of better nutrition (Marshall, 1979). This tendency is taken to the extreme around hydrothermal vents – or 'black smokers' – where rich and varied populations of animals derive nutrition from lush colonies of chemosynthetic bacteria that oxidise sulphides in the hot water gushing from the vents. The nutrition, food webs and feeding strategies of the deep sea are reviewed in Marshall (1979) and Gartner *et al.* (1997).

III. LIGHT IN THE SEA

There are two main natural sources of light in the sea: that provided by the sun, moon and stars, and bioluminescence produced by aquatic animals. Due to the optical properties of water, the prominence and intensity of both sources changes with depth, transforming the visual scene from an extended field of features in the sun-lit shallows to a scene dominated by point-source bioluminescent flashes in the vast darkness of the deep.

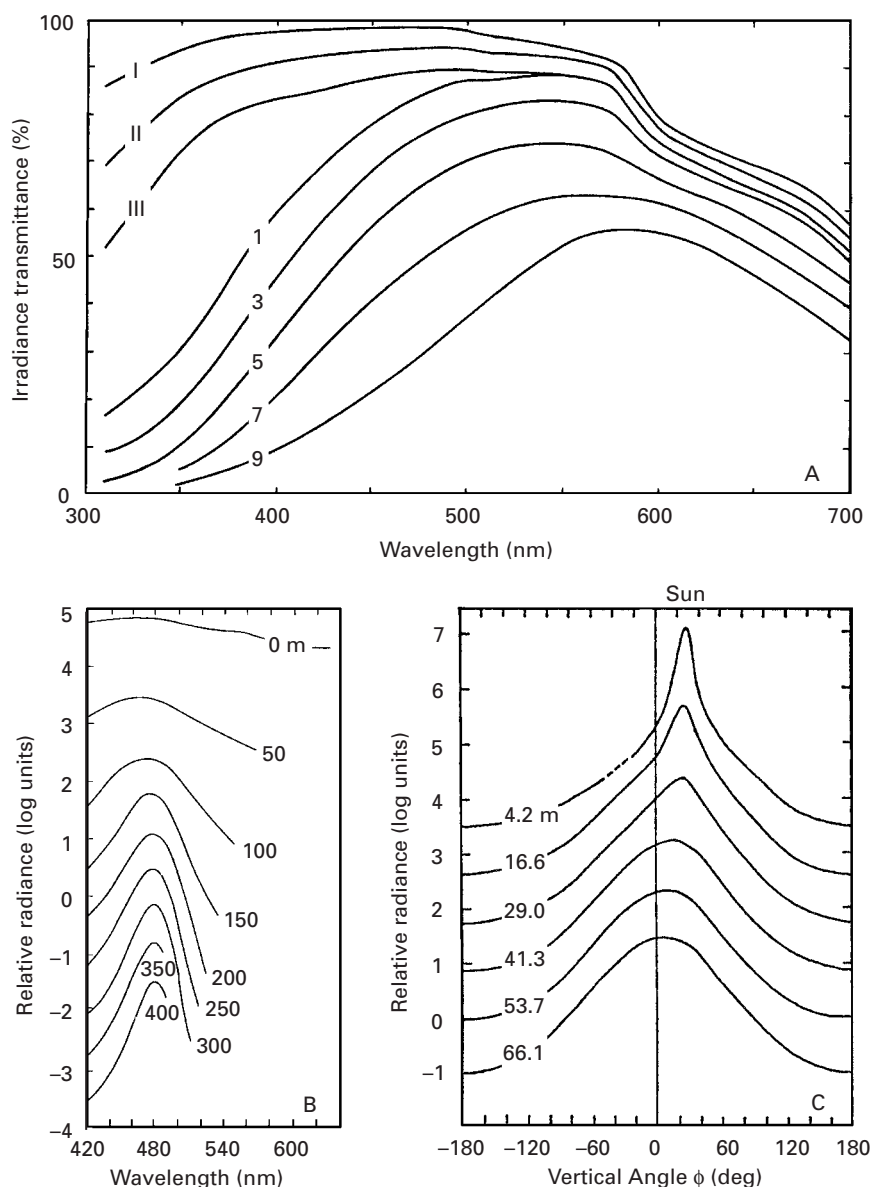


Fig. 1. The properties of light in the ocean. (A) Jerlov's classification of optical water types, based on the quantity and type of dissolved organic matter in the surface layers (transmittance per metre of downward irradiance). The clearest waters are found in the open oceans (types I, II and III), whereas coastal waters and lakes (types 1, 3, 5, 7 and 9) are characterised by greater concentrations of dissolved organic matter and appear more yellow-orange in colour. (B) The relationship between depth (shown in m) and the spectrum of downward irradiance in the Golfe du Lion. (C) The change in the radiance distribution of green light with depth (shown in m) in Lake Pend Oreille. ϕ is the angle relative to vertical (0° = vertical, $\pm 180^\circ$ = horizontal). The distribution is skewed in the direction of the sun near the surface, but becomes more symmetric with increasing depth. In Lake Pend Oreille it becomes perfectly symmetric (asymptotic) at approximately 100 m. Diagrams adapted from Jerlov (1976).

(1) The optical properties of water

Water is an important absorber of light, dramatically reducing its intensity, its spectral composition and its degree of polarisation with increasing depth (Jerlov, 1976). In a clear ocean, the down-welling daylight becomes near-monochromatic blue in colour with increasing depth (Tyler & Smith, 1970). Clear water is most transparent to blue

light of 475 nm wavelength, and within the first 100 m the orange-red part of the spectrum (beyond 550 nm) is almost entirely absorbed (Fig. 1B). Ultraviolet (UV) light is also absorbed, but not quite as effectively: in the clearest oceans, biologically relevant intensities remain down to at least 200 m (Frank & Widder, 1996; Losey *et al.*, 1999). By contrast, light scattered upwards from the depths tends to be relatively rich in UV and shorter wavelengths (Shelton,

Gaten & Herring, 1992). Due to the presence of organic material, coastal waters, creeks and lakes may selectively absorb other wavelengths of light and appear more orange in colour (Fig. 1A; Jerlov, 1976; Lythgoe, 1979; Loew & McFarland, 1990).

Light intensity also decreases dramatically with depth. Although accurate underwater radiance and irradiance measurements are yet to be made on location at mesopelagic depths (Sönke Johnsen, personal communication), we can nonetheless calculate some approximate values. At the surface, the radiance of blue daylight (475 nm) is approximately 2.5×10^{19} photons $\text{m}^{-2} \text{s}^{-1} \text{sr}^{-1}$ (Land, 2000; E. J. Warrant, unpublished data). Using this value at 475 nm and the relative radiance spectrum of surface daylight (Fig. 1B), it is possible to calculate the full quantal spectrum of light at the sea surface, and thereby the number of photons available at the eye from above. Consider an eye whose lens acts as a long-pass filter: in pelagic fishes, it is not uncommon for the lens to block UV with a 50% cut-off at 400 nm (Fritsches *et al.*, 2000). Assume also that the photoreceptors contain rhodopsin molecules with peak sensitivity at 475 nm. Using the calculated quantal spectrum of transmitted daylight, the long-pass properties of the lens and the absorption spectrum of a 475 nm rhodopsin (Stavenga, Smits & Hoenders, 1993), the number of photons available to the rhodopsin molecule from the skylight spectrum is 2.70×10^{21} photons $\text{m}^{-2} \text{s}^{-1} \text{sr}^{-1}$. At 100 m below the surface of a clear ocean the quantal spectrum of daylight has narrowed significantly and is much dimmer (Fig. 1B). A similar calculation reveals that at 100 m the intensity of light available for vision has declined by about 2.6 log units (Jerlov, 1976). This intensity drop varies considerably in different types of ocean water. But at a depth of 100 m in this clear ocean example, 6.8×10^{18} downwelling photons $\text{m}^{-2} \text{s}^{-1} \text{sr}^{-1}$ are available from the surface for vision in an eye with peak sensitivity to blue light (475 nm). Below this depth, presumably because the concentration of plankton and suspended organic matter is less and the spectrum of light is approaching its narrowest, light intensity declines less rapidly: about 1.5 orders of magnitude for every 100 m of depth. It reaches starlight levels (during the day) by approximately 600–700 m (Clarke & Denton, 1962). Below 1000 m almost no daylight penetrates, certainly not enough to be seen by deep-sea animals (Denton, 1990). However, at the mouths of benthic hydrothermal vents the high water temperatures promote chemical processes that emit another (extremely weak) source of visible light (White *et al.*, 2000; Reynolds & Lutz, 2001). The light these processes produce – chemiluminescence, sonoluminescence and triboluminescence – may even be bright enough to be seen. Indeed, as we will see later, the eyes of the vent crab *Bythograea thermydron* possibly have the sensitivity and visual pigment tuning to do just that (Jinks *et al.*, 2002).

The fact that water has a higher refractive index than air means that the entire 180° dome of the sky is compressed to a 97° cone of light underwater. This circular window of light – called ‘Snell’s window’ – provides a bright source of illumination from above (see Walls, 1942). In rough seas this window becomes wider and its edges more diffuse. In still waters, the pattern of polarised light across the dome of the sky – a pattern used by many animals for navigation – is also

visible through Snell’s window, but turbid water and the presence of waves can degrade the pattern significantly (Waterman, 1954; Horvath & Varju, 1995; Cronin & Shashar, 2001). Due to scattering from suspended particles, there is also underwater space light incident from directions outside Snell’s window. Aquatic animals can see this space light both from below and from the side. The space light is strongly polarised in the horizontal plane, but the degree of polarisation declines rapidly with depth (Waterman, 1981), falling to a constant value of between 13 and 38% below the so-called asymptotic depth (see below). Thus, polarised light is potentially available for vision throughout the photic zone (Waterman, 1981), although it is probably most exploited in the upper 200 m (Jerlov, 1976). In clearer water, the space light’s degree of polarisation is higher (Waterman, 1954).

The intensity of light within Snell’s window is always brighter than the surrounding space light, and with increasing depth in a clear ocean, almost all of the daylight available for vision comes increasingly from above (Fig. 1C). This radiance distribution is dominated by the position of the sun in shallow water, but this dominance declines with depth, disappearing altogether below the so-called ‘asymptotic depth’. Below this depth – which is approximately 400 m in clearest ocean water – the radiance distribution is vertically symmetric (Jerlov, 1976). The asymptotic depth is shallower in more turbid water. In Lake Pend Oreille (Idaho, USA) it occurs at approximately 100 m (Tyler, 1960). At this depth space light originating laterally ($\phi = \pm 90^\circ$ in Fig. 1C) and from below ($\phi = \pm 180^\circ$ in Fig. 1C) is respectively about 40 times and 300 times dimmer than light originating directly above ($\phi = 0^\circ$ in Fig. 1C). In clearer water, where the scattered space light is dimmer, these intensity differences are even greater. But regardless of the body of water in question, dim down-welling daylight provides a backdrop against which aquatic animals can spot animals floating above, or against which they themselves can be seen from below. In deep water the most significant light sources in other directions would be bioluminescent.

(2) The changing nature of visual scenes with depth

These changes in the intensity and distribution of light with depth alter the nature of the visual scenes that aquatic animals can see. In the shallower depths, where scattered daylight produces 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 300 times dimmer than that coming from above. Upwards, and even laterally, 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 the scene can be nebulously referred to as semi-extended, becoming less extended 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. It is this change in

visual scene, from the bright sunny layers of the epipelagic zone to the fathomless darkness of the bathypelagic zone, which has arguably had the greatest influence on the evolution of vision in the sea.

IV. THE DESIGNS OF MARINE EYES

Marine animals, no matter at what depth they live in the ocean, rely on a battery of senses to survive. Of these, vision is surprisingly important, even at depths where daylight no longer penetrates.

(1) What do deep-sea animals need to see?

Deep-sea animals use their eyes for many of the same kinds of tasks as their terrestrial relatives. They use vision to orient and to find mates and prey. Vision also helps them to avoid becoming prey themselves. Many deep-sea animals make vertical migrations in the ocean, upwards at dusk and downwards again at dawn, cycling through a range of depths that ensures an environment with a constant light intensity (Widder & Frank, 2001). During this migration they probably use their eyes as optical depth gauges.

In the brighter upper levels of the ocean, the visual task is somewhat similar to that on land. Orientation, and the search for mates, prey and predators, involves the detection and recognition of well-illuminated objects in an extended three-dimensional world. At deeper levels, bioluminescence starts to become important for the identification of mates and prey. These signals are usually point-source flashes, although in some cases they can be considerably larger than point sources, as in the tunicate *Pyrosoma atlanticum*, in jellyfishes that produce remarkable bioluminescent displays around the bell or in crustaceans and cephalopods that eject evasive clouds of bioluminescence (Herring, 2000, 2002). Measurements made at depth reveal that the lengths of flashes may vary from hundreds of milliseconds to several seconds. Their frequency in the sea is generally less than one flash from each steradian (unit solid angle) of water per minute, although frequencies of up to 160 flashes per minute have sometimes been recorded. Below 1000 m flash frequency drops considerably, and becomes very infrequent below 2000 m (Clarke & Hubbard, 1959). It needs to be said however, that these measurements may considerably overestimate flash frequency. The instrument itself, suspended in the water column, has the potential to stimulate mechanically bioluminescence that otherwise may not have occurred.

The intensity and colour of bioluminescent flashes can vary considerably (see Herring, 1978, 2002), but a typical flash is blue 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, most bioluminescent flashes are probably not visible (Denton, 1990).

(2) The eye designs of the deep sea

Nearly all the known eye designs of the animal kingdom can be found in the deep sea, and all have adapted to the

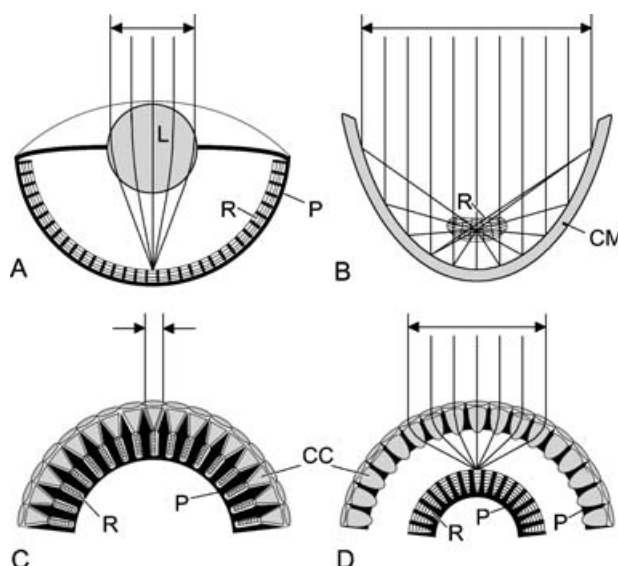


Fig. 2. Aquatic eye designs. (A) Camera eye. (B) Reflector eye. (C) Apposition compound eye. (D) Superposition compound eye (of the refracting type). The arrows indicate the diameter of the pupil through which light reaches the retina. R, retina; L, lens; P, screening pigment; CM, concave mirror; CC, crystal-line cone. From Nilsson (1997).

changing nature of the visual scene with depth. Before we discuss these adaptations, it is necessary to introduce briefly the designs themselves. For a more complete explanation of aquatic eye designs, the interested reader is referred to the lucid reviews of Land (1981*a*, 1990) and Land & Nilsson (2002).

All vertebrates, including those living in the sea, have camera-type eyes (Fig. 2A). So do gastropod and cephalopod molluscs, some annelid worms and certain crustaceans (e.g. copepods). Camera eyes have a retina of photo-receptors that receives an image formed by a lens. In most terrestrial eyes, including our own, the cornea is responsible for most of the refractive power of the eye. The separate lens is responsible for fine-tuning the focus during accommodation. In the camera eyes of aquatic vertebrates (Fig. 2A) the cornea has no refractive power because it separates two media of almost identical optical density, the watery interior of the eye and the surrounding aquatic habitat. In fishes, marine mammals, cephalopods and gastropods, the power of the eye instead comes from a spherical lens that has a gradient of refractive index varying from around 1.52 at the centre of the lens to 1.33 at its surface. Such lenses also tend to be free of the image-degrading effects of spherical aberration. The images formed by these lenses are of excellent quality.

The cephalopod mollusc *Nautilus pompilius* has an eye quite unlike that of other cephalopods in that it has no lens (Land, 1981*a*, 1990; Muntz & Raj, 1984). Its pinhole eye works like a pinhole camera: its small pupil projects a dim image onto a well-organised retina. However, compared to other eyes of the same size, the *Nautilus pompilius* pinhole eye has rather poor sensitivity and only moderate resolution. Nevertheless, the pinhole eye is a significant improvement

on the much more widespread pigment cup eye, which is little more than a pigment-coated cup of photoreceptors, each having a very large visual field. Another odd eye is that possessed by scallops and the ostracod genus *Gigantocypris* (Fig. 2B). In this design light is weakly focused by the cornea, passes through the retina and is then reflected from a concave mirror lining the back of the eye. This reflected light is focused onto the retina, but since the retina has already absorbed some of this light in a weakly focused form, the image contrast is considerably reduced. The concave mirror eye's potential for light capture, on the other hand, is excellent (Land, 1981*a*).

The compound eye is by far the most widespread eye design in the animal kingdom. This design, possessed by arthropods, including insects and most crustaceans, and even some clams and polychaetes, has two main forms: apposition eyes (Fig. 2C) and superposition eyes (Fig. 2D). The former is best adapted for the brighter depths, but as we shall see, they have also evolved for exquisitely sensitive vision in the deep. Like all compound eyes, apposition eyes are composed of up to several thousand similar optical units called ommatidia, each consisting of a lens pair (the cornea and crystalline cone) that focuses light incident from a narrow region of space onto an underlying bundle of photoreceptors (the rhabdom). Each ommatidium is isolated from its neighbours by a sleeve of light-absorbing screening pigment, thus preventing light reaching the rhabdom from all but its own small corneal lens. The denser the packing of ommatidia in a compound eye, the greater the potential for high spatial resolution.

In superposition eyes, a wide optically transparent area (the clear zone) is interposed between the lenses and the retina. In the dark-adapted crustacean superposition eye, screening pigments are compressed around the crystalline cones and near the basement membrane lining the back of the eye. Light adaptation causes the pigments to migrate, thereby reducing light flux at the retina. The clear zone – and specially modified crystalline cones – allow light from a narrow region of space to be collected by a large number of ommatidia (comprising the 'superposition aperture') for focusing onto a single rhabdom, and the images thus formed on the retina are erect. Unlike the crystalline cones of apposition eyes, those of superposition eyes have evolved refractive index gradients as in krill ('refracting superposition eyes'), or reflective surfaces as in crayfish ('reflecting superposition eyes'), or a combination of reflective and light guiding structures as in some crabs ('parabolic superposition eyes'). These crystalline cones allow as many as 2000 ommatidia to collect light for a single rhabdom (as in some large lobsters). Not surprisingly, superposition eyes are common in animals inhabiting very deep water, although they also occur in species (e.g. lobsters and prawns) inhabiting shallow water.

V. THE RELIABILITY OF VISION AT DIFFERENT DEPTHS IN THE OCEAN

As we have already seen, light travelling through water is absorbed and scattered, making the light dimmer and bluer

with increasing distance. For an eye attempting to see something in the deep sea this absorption and scattering has a detrimental effect. With increasing depth, the illuminating daylight is continuously absorbed and becomes ever weaker. Any eye that relies on seeing objects illuminated by such weak light may fail to catch enough photons to create a reliable image on the retina. Even if enough photons are available, scattering of the down-welling daylight by the interposing body of water will create a veiling 'haze' of space light within which the object may disappear from sight. Such scattering greatly limits the furthest distance at which objects may be reliably detected (Lythgoe, 1979, 1988).

(1) Intensity, scattering and visual contrast

Imagine an eye attempting to see a dimly illuminated object without any intervening haze. How reliable is the image formed in the eye? The answer depends very much on the random nature of photon arrivals on the retina. A photoreceptor that absorbs N photons during one integration time will experience an uncertainty – or 'shot noise' – of \sqrt{N} photons associated with this sample, that is, $N \pm \sqrt{N}$ photons (Land, 1981*a*; Warrant & McIntyre, 1993). This noise reduces the reliability of intensity measurements, and thereby discrimination of the contrasts which define spatial details in a scene. The relative proportion of noise ($\sqrt{N}/N = 1/\sqrt{N}$) – and thus the unreliability of vision – will increase with decreasing light intensities (i.e. lower N). In other words, as light intensities fall at greater depths, increasing shot noise levels gradually begin to drown the visual signals. Another reason why vision becomes unreliable at low light levels is that the biochemical pathways responsible for transduction can occasionally be activated in the absence of light (Barlow, 1956). These activations are thermal in origin, produce electrical impulses indistinguishable from those produced by real photons, and are more frequent at higher retinal temperatures. At very low light levels this 'dark noise' can significantly contaminate visual signals, especially in animals whose measured rates of 'dark noise' tend to be high (see Aho *et al.*, 1988). The levels of dark noise in deep-sea animals are unknown, but low water temperatures (approximately 4 °C) probably ensure that rates are rather low. But as we shall see below, these rates are still sufficient to limit the visibility of bioluminescent flashes. Finally, even if a photon is unambiguously absorbed, the small voltage response it produces in the photoreceptor (called a 'quantum bump') is not identical from one photon to the next. Bumps vary in amplitude, latency and duration, and this inconsistency is also a form of noise – called 'transducer noise' – that adds to the uncertainty of vision (Lillywhite & Laughlin, 1979). Again, its amplitude in deep-sea animals remains unknown.

The presence of scattered veiling space light makes the situation for deep-sea vision even worse. Imagine a shark viewing a fish illuminated by down-welling daylight. Light reflected from the fish will radiate towards the shark and create an image of the fish on the shark's retina. Due to the absorption of light by water, the intensity of this image will depend on the range of the fish. If the fish begins to swim away, the intensity of the image will decrease with increasing

distance from the fish. At the same time, the amount of light scattered from the intervening body of water will increase. Both effects attenuate contrast exponentially. Eventually the veiling space light will drown out the light radiating from the fish, and no longer having a discernible contrast, the fish will disappear from sight. For a dark object in the brightest and clearest ocean water, the range at which this occurs is approximately 40 m (Lythgoe, 1979). This range decreases at greater depths when contrast is degraded due to the unreliability of vision in dim light. The visual range around an animal will thus depend on the clarity of the water, the depth at which it lives, and the sensitivity of its eyes. This range will therefore differ from species to species: a successful predator with large sensitive eyes probably relies on having a greater range than its prey, thus spotting its victim before being detected itself (Nilsson, 1997).

Contrast losses due to the dimness and scattering of sea water also take their toll on spatial acuity. Based on the known sensitivity of the human eye, Denton (1990) calculated how well a deep-sea fish might see a small black disc viewed against the down-welling daylight at different depths. The calculation ignores scattering (i.e. the discs were assumed to be at close range) but accounts for the high sensitivity and very clear optics of fish eyes. A deep-sea fish with a pupil area of 0.5 cm^2 and retinal wiring similar to that of a dark-adapted human, should be able to distinguish a disc subtending a visual angle as small as 10 minutes of arc at a depth of 600 m. In brighter, shallower water, discs of smaller size should be visible. However, in dimmer water at greater depths the decreased signal-to-noise ratio will increase the minimum detectable size of the disc.

Our discussions so far all hint at one major conclusion: good spatial acuity and a long visual range – and thus a competitive edge in the struggle for survival – can only be achieved when an eye captures as much of the available light as possible. A more sensitive eye has a better chance of securing reliable vision by overcoming photon noise. The strategies employed for increasing sensitivity depend very much on what an animal needs to see in order to survive. Eye designs for maximum sensitivity to point-source bioluminescent flashes are quite different to those for maximum sensitivity to the extended down-welling daylight. Both types of stimuli are commonplace in the ocean, and some species need to see both equally well. This is no doubt in part responsible for the bewildering variety of eye designs that perplexed Murray and Hjort in 1912.

(2) The sensitivity of eyes to extended sources

The features of eyes that maximise their sensitivity to dim extended scenes have been nicely summarised by Land (1981*a*). In short, good sensitivity to an extended scene results from a pupil of large area ($\pi A^2/4$), and photoreceptors each viewing a large solid angle ($\pi d^2/4f^2$ steradians) of visual space and absorbing a substantial fraction of the incident light ($1 - e^{-kl}$ for monochromatic light). Here A is the diameter of the pupil, f the focal length of the eye, and d , l and k the diameter, length and absorption coefficient of the

photoreceptors, respectively. If all lengths have units of μm , then k has units of μm^{-1} . The optical sensitivity S of the eye to an extended monochromatic scene (in units of $\mu\text{m}^2 \text{ sr}$) is then simply given by the product of these three factors (Kirschfeld, 1974; Land, 1981*a*):

$$S = \left(\frac{\pi}{4}\right)^2 A^2 \left(\frac{d}{f}\right)^2 (1 - e^{-kl}). \quad (1)$$

Wider pupils, larger photoreceptors or shorter focal lengths all increase S . We shall see that these are common features of mesopelagic eyes that view objects in the dim extended space light. The total number of photons N absorbed per second by a photoreceptor viewing an extended scene of radiance L photons $\mu\text{m}^{-2} \text{ sec}^{-1} \text{ sr}^{-1}$ is then simply

$$N = L \cdot S. \quad (2)$$

Eyes of greater sensitivity absorb more photons from an extended scene of given intensity.

Sensitivity can be dramatically improved by increasing the solid angle of space that is seen by each visual channel (which is proportional to d^2/f^2 ; equation 1). So far we have defined the isolated photoreceptors as the visual channels, but these view very small solid angles. This is because of their small diameter d , which is never greater than a few micrometres. How then can the solid angle be increased? The most effective way is to pool – or sum – the outputs of groups of neighbouring photoreceptors. This creates larger ‘effective channels’, each viewing a larger solid angle of visual space. Such spatial summation greatly improves the sensitivity of the eye, but only at a price: larger solid angles result in a coarser view of the world and a degraded spatial resolution. In the vertebrate retina it is the ganglion cells that are ultimately responsible for summing signals from the photoreceptors, and it is they which determine the matrix of visual channels that sample a scene (Hughes, 1977; Collin, 1999). The size of a ganglion cell’s receptive field – and thus the solid angle of visual space that it views – is proportional to the number of photoreceptors that it pools.

Eyes can also increase their sensitivity by increasing the visual ‘exposure time’ for capturing a sample of photons, just as a camera can in dim light. Longer exposure times result in a greater photon catch, but only at the expense of fast vision. This temporal summation is typical of nocturnal animals (e.g. Aho *et al.*, 1988) and is probably widespread in the darkness of the deep sea. Despite the costs, the extra photon catch afforded by spatial and temporal summation dramatically improves the visibility of a dim extended scene (Warrant, 1999).

(3) The sensitivity of eyes to semi-extended and point-like sources

An eye that strains to see bioluminescent point sources should be designed somewhat differently. By definition, a point-source object creates a point-source image on the retina (assuming that aberrations and diffraction do not blur the image too much). Such an eye wins nothing by having visual channels that view large solid angles of space. For a

channel to catch all the light from a point-source image, its receptive field need not be any larger than the image itself. A single photoreceptor is probably more than adequate for this. Spatial summation – a useful strategy for extended scenes – would now be quite useless.

But before considering sensitivity, we need to ask whether the images of point sources really are smaller than the receptive fields of visual channels in the retina. If we assume that aberrations are negligible (which they are: Ronald Kröger, personal communication), then the size of a 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 (for an average bathypelagic pupil: Warrant, 2000), then the width of the image is approximately 0.5 arc min, which is ten times smaller than the receptive fields of foveal ganglion cells in many bathypelagic deep-sea fishes (approximately 5 arc min: Warrant, 2000). For a 1 mm pupil, the image is significantly wider, around 4 arc min, but this is still smaller than a ganglion cell receptive field. The following calculations of sensitivity assume that the point-source image falls entirely within the receptive field of a foveal ganglion cell. As we will discuss below, multiple scattering phenomena may prevent this from happening, but as yet the effect of this is unknown.

In the bathypelagic darkness, a bright pin-point of bioluminescent light will be highly visible to any eye with a large pupil area. If the point source is located r metres from an eye of pupil diameter A , and contains a total of E photons at source, then it is easy to show (Warrant, 2000) that the number of photons N that enter the eye, and are absorbed by a photoreceptor, is

$$N = \frac{EA^2}{16r^2} e^{-\alpha r} (1 - e^{-kl}). \quad (3)$$

The first exponential term describes the attenuation of the bioluminescent flash due to the scattering and absorption of light by water, and α is the combined attenuation coefficient (Lythgoe, 1979). For clear water and blue light, $\alpha=0.05 \text{ m}^{-1}$ (Denton, 1990). We have already seen the bracketed term – the fraction of incident monochromatic light that is absorbed by a photoreceptor – in equation (1). According to equation (3), smaller pupils, or bioluminescent flashes that are further away, will reduce the photon catch and decrease the reliability of vision.

How far away can a bathypelagic fish with a certain pupil size perceive a bioluminescent flash of given intensity? If it were not for the presence of spontaneous isomerisations (i.e. dark noise) in the photoreceptors, eyes could theoretically detect flashes infinitely far away. Even low rates of dark noise will eventually swamp the real signals generated by photons arriving from an increasingly distant flash. If the dark noise rate is X ‘false photons’ per second, then following the logic of Land (1981*a*), N photons entering the eye from a bioluminescent flash can be distinguished from the dark noise with 95 % reliability when

$$N \geq 1.96\sqrt{2X}. \quad (4)$$

For threshold detection, equations (3) and (4) can now be equated:

$$\frac{EA^2}{16r^2} e^{-\alpha r} (1 - e^{-kl}) = 1.96\sqrt{2X}. \quad (5)$$

In frogs, $X=0.011 \text{ s}^{-1}$ at 16°C , and this rate falls by slightly more than a factor of ten for every 10°C drop in temperature (Aho, Donner & Reuter, 1993). Assume that in the very cold (4°C) waters of the deep sea, photoreceptors have a dark noise of $X=0.0001 \text{ s}^{-1}$. Let us also assume that the photoreceptor absorbs all the light that is incident upon it (i.e. the bracketed term in equation 3 equals 1). Imagine the fish has an average bathypelagic pupil and sees a blue bioluminescent flash of average intensity ($A=7.3$ mm, $E=10^{10}$ photons, and $\alpha=0.05 \text{ m}^{-1}$: averaged for several species – Warrant, 2000). With these values, we can now solve equation 5 numerically to obtain $r=97$ m. In other words, a fish with a 7.3 mm wide pupil will see the flash at distances up to 97 m away. If the rate of dark noise is ten times larger, the maximum distance is reduced to approximately 80 m. Of course, these calculations assume rather ‘ideal’ conditions, including an extrapolated rate of dark noise. Moreover, we have only accounted for dark noise, and ignored other forms of noise including photon shot noise and transducer noise. In reality, the maximum visible distances for bioluminescent flashes are probably a lot shorter than those calculated here. Maximum visible distances are plotted for different flash intensities and pupil diameters in Fig. 3A. Brighter flashes can be seen further away, but even for the brightest flashes and the largest pupils, the maximum range of visibility, with the assumed rate of dark noise, is approximately 230 m. The consequences of this for vision in bathypelagic fishes will be discussed later.

What happens to point source detection in the semi-extended world of the mesopelagic zone? In the dark world of the bathypelagic, bioluminescent flashes stand out easily. But at shallower depths, bioluminescent sources have to compete with the intensity and scattering of the surrounding space light. When the space light becomes brighter, bioluminescent signals lose their contrast and are eventually drowned out. The depth D at which this occurs depends on the sensitivity of the eye, the direction of sight and the intensity and range of the flash. Let us assume that visual discrimination is limited by both photon shot noise and dark noise, and that below a depth of 100 m space light intensity decreases by 1.5 log units for every further 100 m of depth (Section III). Also assume that the space light intensity is insufficient to saturate the rods. It can be shown that the shallowest depth (D_u metres) at which a bioluminescent flash can be seen in an upward direction against the down-welling daylight is (Appendix A):

$$D_u = 100 - 66.7 \log_{10} \left\{ \frac{1}{L_o} \left(\frac{4f}{\pi A d} \right)^2 \left[\left(\frac{EA^2 e^{-\alpha r}}{44.3r^2} \right)^2 - X \right] \right\}. \quad (6)$$

The flash is assumed to have a duration equal to the integration time of a rod. L_o is the number of down-welling photons $\text{m}^{-2} \text{ s}^{-1} \text{ sr}^{-1}$ at 100 m depth that are available

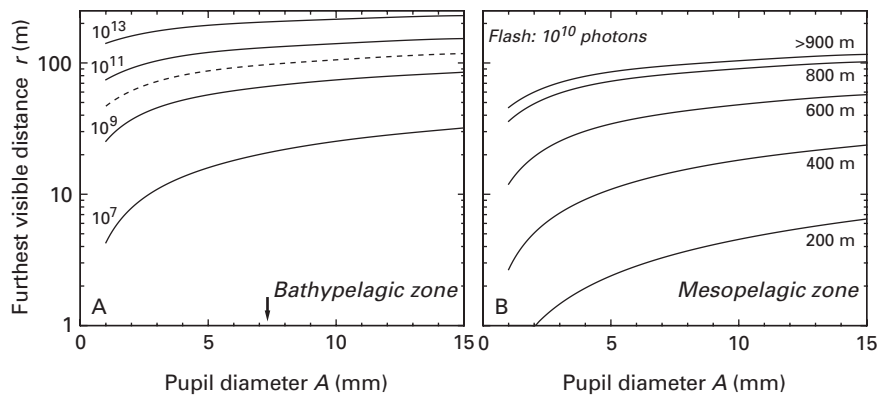


Fig. 3. The visibility of bioluminescent point sources in the ocean for fishes of pupil diameter A . The furthest distance r that a fish can see a given point source is plotted as a function of A . (A) Visibility in the bathypelagic zone for flashes of different intensities (solid lines, 10^7 – 10^{13} photons; dashed line, 10^{10} photons, an average intensity). The arrow marks an average bathypelagic pupil diameter of 7.3 mm. (B) Visibility against background light at different depths in the mesopelagic zone (200 to >900 m) for a 1 s flash containing 10^{10} photons.

from the surface for vision in an eye with peak sensitivity to blue light (475 nm). This is approximately 6.8×10^{18} photons $\text{m}^{-2} \text{s}^{-1} \text{sr}^{-1}$ (see Section III above). All other symbols have their usual meanings and units. The shallowest depth that an eye can just see the flash laterally, where space light is 40 times dimmer, is ($D_u - 107$) m. Downwards, where the space light is 300 times dimmer, the shallowest depth is ($D_u - 165$) m. Notice that bioluminescent flashes are better detected against the background space light when the pupil is larger (αA^2), the photoreceptor visual fields are smaller ($\alpha d^2/f^2$), or when the flash is brighter and closer. In other words, the best detection occurs with a larger and sharper eye for flashes that are brighter and closer.

Take the average fish eye and flash intensity we considered earlier [$A = 7.3$ mm, $E = 10^{10}$ photons (1 s flash) and $\alpha = 0.05 \text{ m}^{-1}$]. For simplicity, we will allow the pupil to be the same diameter as the lens. Let us presume that the eye is also built according to Matthiessen's principle (1882), with a focal length about 2.5 times the radius of the lens (i.e. $f = 1.25A$: a smaller pupil is equivalent to a smaller eye). If the eye has a rod photoreceptor diameter d of $3 \mu\text{m}$, a dark noise X of 0.0001 sec^{-1} and the flash is 5 m distant ($r = 5$ m), then $D_u = 249$ m. Thus, at a depth of 249 m a flash containing 10^{10} photons would not be visible beyond 5 m. The space light masks the flash if it is further away. Imagine a fish with a 3 mm pupil ascending from great depths. As it ascends, the fish would be able to distinguish a flash located 15 m away until a depth of 508 m, above which the flash would be masked by the space light. A flash located 5 m away would be seen until the fish ascends to a depth of 352 m. With a 7.3 mm pupil, the fish would be able to see a flash located 15 m away until it ascends to a depth of 405 m. In other words, flashes further away seen by smaller eyes disappear from view at greater depths. The furthest distance that a flash containing 10^{10} photons can be detected against the space light is plotted for different depths and pupil diameters in Fig. 3B.

As indicated earlier, these calculations of sensitivity assume that the point-source image falls entirely within the

receptive field of a foveal ganglion cell. This, however, may not be the case. Light emitted from a point source in a scattering medium like water may be scattered more than once, that is, it may suffer from 'multiple scattering' (Sönke Johnsen & Edith Widder, personal communication). A ray of light that initially travels in a direction that the eye does not view, may return to the eye's field of view by being scattered back into it. Such rays could potentially smear the image, and create a haze around it, much like the appearance of a car headlight in fog. This blur-circle image could easily be larger than the receptive field of a foveal ganglion cell, and depending on the nature of this multiple scattering (presently unknown: S. Johnsen & E. Widder, in preparation), the enlarged image may also be somewhat dimmer. If it is, then the source may be less visible, and its range for threshold detection closer than the ranges calculated above.

(4) The spatial resolution of deep-sea eyes

Exquisite sensitivity is not the only quality required of deep-sea eyes. Most eyes also need to determine the directions from which light has arrived, that is, to discern its spatial distribution. In the brighter upper depths, the colour and polarisation of the illuminating daylight are also important, but these are much less meaningful in the deep sea. The ability of an eye to determine the spatial distribution of lighter and darker areas of illumination – in other words, to resolve images – depends on the optical quality of the eye and the physical arrangement of the eye's visual sampling channels. The density of these channels, and the sizes of their receptive fields, sets the spatial resolution of the eye. This channel density may vary in different parts of the eye's field of view, so that some areas of the visual world are better resolved than others, which generally reflects some aspect of the animal's ecology.

In a bright diurnal terrestrial environment, where light levels are not limiting, eyes with high resolution are commonplace. In compound eyes, the visual channels are defined by the ommatidia, and areas of the eye where they are

densely packed – known as ‘acute zones’ – view the world with high spatial resolution. These acute zones are used in a variety of behavioural contexts, including the detection of mates and prey, the fixation of a feature in the habitat (such as the horizon), and to match the pattern of optic flow during flight (for reviews, see Land, 1989*b*, 1999; Warrant, 2001; Land & Nilsson, 2002). Acute zones may be uncommon in deep-sea crustaceans (apart from those, like hyperiid amphipods, that need to localise point sources – see below), although very little work has been done on this topic. The high sensitivity required to view a dim extended scene does not favour acute zones. Even if they do exist, they will almost certainly be confined to apposition eyes (in fact a slight acute zone is seen in the apposition eye of the deep-water ostracod *Macrocypidina castanea*: Land & Nilsson, 1990). Except for the remarkable case of some diurnal hawkmoths (Warrant, Bartsch & Günther, 1999) and the strange detached mini-retina of a shallow living mysid (Nilsson & Modlin, 1994), acute zones are unknown in superposition eyes.

In the camera eyes of fishes (and indeed all vertebrates), the visual channels are defined by the array of retinal ganglion cells (Hughes, 1977), whose density varies throughout the retina. These cells represent the final level of processing in the retina, their axons carrying visual information to the brain via the optic nerve. Each ganglion cell receives inputs from a pool of photoreceptors – typically rods in deep-sea fishes – via a network of bipolar cells. The size of the photoreceptor pool effectively sets the size (and sensitivity) of the dendritic receptive field of a single ganglion cell at a given point in the retina (Copenhagen, Hemilä & Reuter, 1990). Smaller pools (and smaller receptive fields) imbue higher resolution but are also less sensitive. An area of the retina where the receptive fields are smallest represents the ‘acute zone’ of the vertebrate retina. Known as the ‘area centralis’ in fishes, this retinal region has the greatest density of ganglion cells and the highest spatial resolution vision (see for example Fig. 11). In many species, the most tightly packed cells of the area centralis also line a deep pit-like structure known as the ‘fovea’ (see Fig. 14B).

The word fovea means ‘pit’, and well describes the structure found in a number of deep-sea fishes. These deep foveae, called convexiticulate by Walls (1937, 1942), occur in a wide variety of vertebrate eyes, including those of birds of prey, swallows and kingfishers, chameleons, pipefishes and seahorses. Similar structures are also found in the retinæ of jumping spiders. Foveae are found in at least 50 species of deep-sea fishes, although they have not been reported in elasmobranchs.

In all these cases there is a marked depression in the vitread contour of the retina, reflected in some cases by a corresponding bulge, a fovea externa, on the sclerad surface as well. Inspection of the position of the fovea in the retina shows that it is aligned with some point in the periphery that is of visual importance to its owner. Some birds of prey have two such foveae in each eye, one is directed forwards, the other laterally. The deep-sea fishes with foveae have only one in each eye, located in the periphery, and are able to subserve a binocular function. This is also seen in shallow-living pipefishes and seahorses. Before considering their function further, we need to examine a typical deep-sea fovea. The

platytroctid and alepocephalid fishes provide good examples (the deep convexiticulate fovea of the alepocephalid *Conocara macroptera* is shown in Fig. 14B). Radial sections show that the vitread contour of the retina is lined with a dark-staining material derived from radial (Müller’s) fibres. The dark staining suggests that the optical density of this lining is higher than that of the adjacent retina. The pit itself is of characteristic contour, sloping inwards to a steeply concave bottom. Sclerad to the pit, the retinal elements are markedly thinned, with the nuclei of the inner and outer nuclear layers, as well as the synaptic pedicles of the visual cells (all rods in all but a few cases) swept to the sides. The foveal photoreceptors are thinner, longer and more closely packed than those of the peripheral retina.

Apart from their occurrence in such disparate animals, it is remarkable that the absolute size of foveae across the range is very similar. The pit is approximately 300 μm across the shoulders, and the foveae of the 14 mm larval smooth-head *Alepocephalus agassizii* and the adult wedge tailed eagle *Aquila audax* are of comparable size. This is the case even though the fish could swim about within the eagle’s eye! Since the receptor diameter does not vary greatly across foveate species, the architecture of the fovea is probably related to receptor dimensions rather than to the size of the eye containing the fovea.

The deep foveae of vertebrate eyes have evolved to subserve fine spatial resolution. The superior spatial resolution found in birds is certainly the result of such foveae. Falcons have been shown to have a visual acuity twice that of humans, and the role of the fovea in achieving this has previously been discussed by Snyder & Miller (1978). The human fovea is also concerned with fine detailed vision, but is not of the deep type, and depends on receptor size and neural connections for its quality. As in humans, the bird fovea has narrow receptors, and probably fine grain connectivity, but the shape and nature of the bird’s deep foveal pit also plays a role. Light passing through the retinal layers of the fovea is affected by two factors: the difference in optical density between the vitreous humour and the retina, and the curvature of the foveal slope. A cone of light approximately 20° wide, as produced by the lens of a bird of prey, will fall within the pit if centred there, and then diverge due to the steep concavity at the bottom. This will produce a magnified image on the array of photoreceptors, with potential for increased resolution. Ray tracing suggests that a cone of 40°, as in fishes that conform to Matthiessen’s ratio, will still be brought to a sharp focus when centred. Even though the resolution of such fish eyes is likely to be limited by neural rather than optical considerations, magnification will still occur. The fovea will spread the image of a bright point source over a larger number of receptors than would have been the case without the fovea, providing greater opportunity for neural convergence.

(5) The trade-off between spatial resolution and sensitivity

Sensitivity to a dim extended scene generally comes at the expense of good spatial resolution (Warrant & McIntyre, 1992). This assumes that eye size is constrained, which it

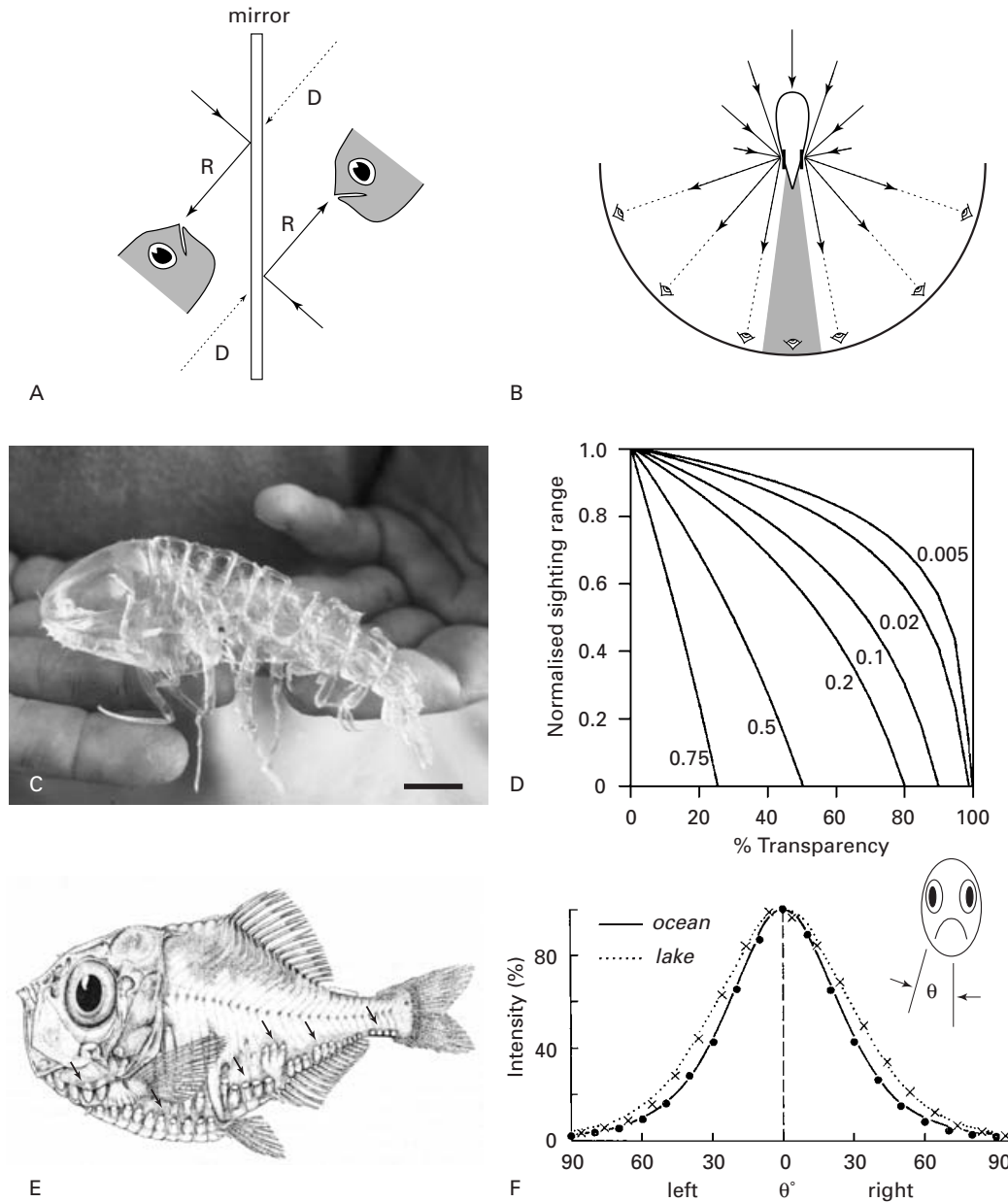


Fig. 4. Camouflage strategies in the mesopelagic zone. (A,B) Silvering, (C,D) Transparency, (E,F) Bioluminescent counter-illumination. (A) A fish looking at a flat vertical mirror will find it impossible to distinguish between direct (D) and reflected (R) light. The mirror thus appears invisible. Re-drawn from Bone, Marshall & Blaxter (1995). (B) Fishes camouflaged by silvering possess reflective scales that are oriented vertically irrespective of the curvature of the fish's flanks. The fish will only be visible directly from above or from below (shaded), assuming no other form of camouflage is present. From other directions the fish will be invisible. Re-drawn from Denton & Nicol (1966). (C) The transparent mesopelagic amphipod *Cystisoma* sp. Despite being visible in the lower refractive index of air, this animal is virtually invisible in water. Scale bar = 1 cm. Photograph courtesy of Dan-Eric Nilsson. (D) The relative sighting distance of a transparent prey animal as a function of its % transparency, for predators of different minimum contrast thresholds for object detection ($C_{min} = 0.005\text{--}0.75$). Relative sighting distance is defined as the actual sighting range for an animal divided by the sighting range for an opaque object, a measure that controls for water clarity, prey shape, prey size etc. For any given predator (C_{min} constant), prey that are more transparent have shorter sighting distances (i.e. they remain undetected until the predator is very close). For any given prey animal (% transparency constant), predators able to perceive smaller contrasts (i.e. with lower C_{min}) are able to see the prey further away (and thus have a better chance of detecting them). Adapted from Johnsen & Widder (1998). (E) The hatchet fish *Polyipnus laternatus* (approximately 40 mm long), showing the batteries of photophores along its ventral surface (arrows). Drawing from Marshall (1979). (F) The relative intensity of counter-illumination at different lateral

usually is, either because of the finite size of the animal or for energetic reasons. We shall soon see that there are some animals – like the giant deep-sea squid *Architeuthis dux* – which maintain enormous eyes, and have pupil diameters and focal lengths that assure high sensitivity and sharp spatial resolution. For a given eye size however, larger pupils suffering aberration, wider photoreceptors and pronounced neural summation – all desirable for maximising photon capture – usually compromise the quality of images focused on the retina and coarsen the neural sampling matrix. But in the deep sea, where small animals strain to capture light, it is certainly better to see a dim coarse world than nothing at all.

Large reflecting superposition eyes, like those found in a deep-sea lobster, could easily have a very sensitive superposition aperture comprised of hundreds, or even thousands, of ommatidia that capture light for a single rhabdom. A small insensitive aperture, containing just a few tens of ommatidia, would probably have no difficulty aiming the individual pencils of light, originating from each lens, so that they superimpose exactly on a single photoreceptor. The large aperture of the lobster, having evolved in the quest for photons, would probably do a much worse job of focusing light, and the blurry image formed on its retina would irreparably degrade spatial resolution. Some extreme eye designs appear to have tipped the trade-off almost entirely in favour of sensitivity, being constructed for the sole purpose of merely detecting the presence of light, rather than accurately to distinguish from where it came. The reflector eyes of the ostracod genus *Gigantocypris* (Fig. 2B) are a good example.

The same trends can be seen in mesopelagic fishes. As we shall see below, the retinæ of mesopelagic fishes that need to distinguish objects in the dim down-welling daylight usually have a retinal construction that favours sensitivity, an adaptation that becomes more obvious with increasing mesopelagic depth. The sharp foveae that are common in fishes from the bright epipelagic layers are replaced by a coarser and more uniform matrix of ganglion cells in fishes from the mesopelagic zone. These ganglion cells have wide and sensitive receptive fields, collecting inputs from large pools of rods. Such a construction does not permit high spatial resolution.

But the trade-off is not always tipped in favour of sensitivity, especially if the light to be detected is a point source of high contrast. For high-contrast point sources – either bright against a dark background or *vice versa* – good spatial resolution is essential if they are to be accurately localised. The acute zones of hyperiid amphipod compound eyes, used for localising small targets silhouetted in the down-welling daylight, are excellent examples, as we shall see below. So too are the surprisingly well-developed foveae of bathypelagic deep-sea fishes, which are superbly adapted for localising points of bioluminescence.

VI. ADAPTATIONS FOR VISION IN THE MESOPELAGIC ZONE

Of all the environments of the ocean, the mesopelagic zone is the most varied from the point of view of vision. Spanning a daylight intensity range of approximately 13 log units, and home to countless bioluminescent organisms, the 850 m of the mesopelagic zone encompass the entire range of visual scenes – from extended to point source – which an eye might encounter. This fact is reflected in the visual adaptations of mesopelagic animals, which are unquestionably the most varied found in the ocean.

(1) The visual world of the mesopelagic zone: seeing without being seen

Unlike terrestrial habitats, the vast open ocean offers no refuge for its inhabitants, no places to hide. The featureless infinity of blue light, brightest above and darkest below, provides a uniform background against which all objects can be revealed. Some objects will be brighter than this background. Some, like silhouetted objects seen above, will be darker. But whether darker or lighter, a body that contrasts with the background is a potentially dangerous liability. Not surprisingly, mesopelagic animals have evolved a suite of adaptations to decrease or even eliminate their own contrast, thereby significantly increasing their chances of remaining undetected. Even modest reductions in contrast can make an animal very difficult to detect (Land, 2000).

In the mesopelagic zone, this type of camouflage usually takes one of four possible forms: cryptic colouration, transparency, silvering or bioluminescent counter-illumination (Fig. 4; Nilsson, 1997; Herring, 2002).

(a) Cryptic colouration

In the bright upper levels of the ocean, where the down-welling light still has a relatively broad spectrum, many animals camouflage themselves by being blue. Several crustaceans and cnidarians achieve this colour with chromatophores filled with blue carotenoprotein pigments. Others achieve it by Tyndall scattering, as in some isopods. Deeper down, in the upper mesopelagic zone, many animals begin to take on a reddish appearance, a colour that absorbs the incident blue light rather well. Larger shrimps are 'half-red', sparsely pigmented along their otherwise transparent dorsal surfaces with a few rather large red chromatophores. From above, these pigments make them appear darker, thus better matching the darker water below. Some red pigmentation is however also seen on the ventral and lateral body surfaces, which may camouflage the shrimp if illuminated by bioluminescence. In the lower mesopelagic depths below 600 m, the red pigmentation of shrimps becomes more intense, allowing them to appear as dark as the

angles (θ), relative to the downward vertical direction ($\theta=0^\circ$), for two mesopelagic fishes: the viper fish *Chauliodus sloani* (×) and the hatchet fish *Argyrops affinis* (●). The angular distribution of counter-illumination is remarkably similar to that found in the ocean (solid line) and in Lake Pend Oreille (dotted line), and thus provides excellent camouflage. Adapted from Denton *et al.* (1972).

ever-darkening background. Many medusae take on red, brown or even purple colouration for the same reason. Fishes too become darker. In the bathypelagic darkness below 1000 m, animals tend to become uniformly dark. Fishes take on a velvety black appearance (due to melanin pigments), crustaceans are a uniform scarlet and medusae are a deep chocolate purple-brown. These colours have no meaning in the bathypelagic zone apart from their role in camouflage. Blue bioluminescent flashes are absorbed by these colours, and if illuminated, dark bathypelagic animals appear invisible against the blackness beyond.

Despite its apparent simplicity, cryptic colouration is not a trivial form of camouflage. Its success depends on a number of factors, especially viewing angle and depth, as recently shown in an elegant study by Johnsen (2002).

(b) *Silvering*

Opaque mesopelagic animals can make themselves appear transparent by having bodies covered in silvery mirrors (Fig. 4A,B). A flat vertical mirror will appear invisible at all angles of view (except exactly from above or below) in the predictable vertically symmetric down-welling light found at asymptotic depths in the sea. The effect is also independent of intensity, and therefore independent of depth.

Among the best known users of this strategy are the leaf-like mesopelagic hatchetfishes, whose vertically flattened silvery sides – created by multiple stacks of guanine crystal sheets – reflect almost 100% of the incident light, and endow them with a stunning metallic sheen (Denton & Land, 1971; Land, 1972). At night however, when the predictable vertical light distribution dims by eight or nine orders of magnitude, the mirrored flanks of hatchetfishes place them at considerable risk: a well-aimed flash of predatory bioluminescence would reveal a hatchetfish by its bright reflection. To prevent this from happening, many species of hatchetfishes have dark chromatophores that disperse pigment over the mirrors at night (Herring, 2002).

(c) *Transparency*

A highly effective strategy to minimise or eliminate body contrast is to be transparent (Fig. 4C,D). As simple as this strategy sounds, the mechanisms used to achieve transparency are not at all trivial (Johnsen & Widder, 1998, 1999; Johnsen, 2001). Nonetheless there are many groups of animals – spanning across most phyla of the animal kingdom – that reach remarkable levels of transparency (Johnsen, 2000, 2001).

To be perfectly transparent, an animal must have the same transmission and reflection characteristics as the surrounding water (i.e. the same refractive index). This would mean having a body composed of sea water, which of course is impossible: the epidermis and internal organs of animals, and the unavoidably opaque contents of their digestive tracts, prevents this from ever occurring. Nevertheless, many gelatinous mesopelagic animals (such as jellyfishes, which can achieve 91% transparency; Johnsen & Widder, 1998) incorporate sea water into their tissues in order to minimise the refractive index difference (Herring, 2002).

However, some tissues must remain opaque by necessity. The retinæ of eyes, for instance, must retain light-absorbing visual pigments in order to see. In some animals this has been partially overcome by eliminating screening pigments, as in the amphipod *Cystisoma* sp., or by drastically reducing the volume of the retina to the minimum necessary, thus confining the revealing contrast to as small a region as possible. This is the strategy adopted by the lower mesopelagic amphipod *Phronima sedentaria*, which has remarkable compound eyes that each supply light to a tiny pigmented retina via an elaborate system of light-guiding lenses (see below). Another strategy to overcome internal opacity is to have a very flat blade-like or leaf-like body, within which the organs and gut contents are thinned out over a wide area (Johnsen, 2001). The wafer-thin larvae of some lobsters and fishes are excellent examples.

Apart from these adaptations, there are also structural mechanisms that ensure the extreme clarity of tissues. If carefully and regularly ordered, cellular structures (such as muscle fibrils and protein matrices) can ensure the destructive interference of scattered light, thereby rendering the constituent tissue transparent (Johnsen & Widder, 1999; Johnsen, 2001). The corneas and lenses of vertebrate eyes achieve their clarity via this mechanism. Transparency may also be achieved if the surfaces of animals are covered in submicroscopic protrusions. These provide clarity by mimicking a material whose refractive index is intermediate between that of sea water and that of the epidermis. This mimicry provides the body surface with an anti-reflection coating which eliminates light that might otherwise reach a predator's eye (Johnsen, 2001). In marine animals these structural strategies can endow near-perfect transparency, in fact so near that a human observer would have difficulty seeing them (Johnsen & Widder, 1998, 1999; Johnsen, 2001). No doubt this difficulty is equally great for many potential predators.

How well camouflaged are transparent mesopelagic animals? The answer to this question depends almost exclusively on the animal's degree of transparency, that is, on its inherent contrast at zero distance, C_o (Johnsen, 2001):

$$C_o = \frac{L_{ob} - L_b}{L_b}, \quad (7)$$

where L_{ob} is the radiance of the object, and L_b is the radiance of the background. If the object is darker than the background, C_o is negative, otherwise C_o is positive. Transparency T is simply given by $1 - |C_o|$.

Semi-transparent animals, with a small but distinct contrast, will be detected at greater distances by predators and prey than near-transparent animals with little or no contrast. To see a near-transparent animal, the viewer must be a lot closer. The distance at which a transparent animal can just be seen is referred to as its 'sighting distance' (d_{sighting}). Transparent prey animals with shorter sighting distances than those of their predators have a better chance of escaping detection. Transparent predators with shorter sighting distances than their prey have a better chance of intercepting the prey without being noticed. The sighting distance depends (Johnsen, 2001) on the contrast (transparency) of the animal (C_o), the threshold minimum contrast

detectable by the viewer's eyes (C_{\min}), and the light transmission characteristics of sea water (attenuation coefficient of the background radiance, K_L , and the beam attenuation coefficient of water, c):

$$d_{\text{sighting}} = \frac{\ln\left(\frac{C_0}{C_{\min}}\right)}{c - K_L}. \quad (8)$$

Although not indicated, the values of all parameters in equations (7) and (8) depend on the wavelength of light [e.g. $K_L(\lambda)$].

Inspection of equation (8) shows that sighting distance is smaller for more transparent animals (lower C_0), or for a viewer whose eyes have a higher threshold contrast C_{\min} (Fig. 4D). The water quality is also important: murkier water (higher K_L and c) leads to shorter sighting distances, and effectively veils an animal from sight. C_{\min} has been determined in bright light for a number of fishes, and varies between approximately 0.01 and 0.07 depending on species (Johnsen, 2001). In man, $C_{\min} \approx 0.01$. In dimmer light, the ability of animals to distinguish contrast diminishes due to the presence of visual noise. This means that in dimmer light, or at greater depths in the ocean, C_{\min} increases. In the cod *Gadus morhua*, for instance, C_{\min} increases from 0.02 near the surface to 0.5 at 650 m (Anthony, 1981). Sighting distance and detectability therefore vary with depth: a semi-transparent animal visible near the surface may become invisible at depth [see Johnsen & Sosik (2003) for examples of sighting distances calculated for the cod at different depths and times of day, and in various water types].

(d) Bioluminescent counter-illumination

Many mesopelagic animals, notably fishes, cephalopods and crustaceans, have a battery of photophores along the ventral body surface (Fig. 4E), each of which produces bioluminescence that mimics the colour (see Fig. 13D), intensity and angular distribution (Fig. 4F) of the surrounding down-welling daylight (Denton, Gilpin-Brown & Wright, 1972; Denton *et al.*, 1985). This clever trick – known as bioluminescent counter-illumination – can effectively eliminate an animal's silhouette.

The hatchetfishes are excellent examples: large tubular photophores cover the ventrally projecting surface of the entire body. These are lined with a reflective silvery coating, and their exit apertures are plugged with magenta-coloured filters (Denton, 1970). This results in a blue bioluminescent light that is remarkably well matched to the colour and angular distribution (Fig. 4F) of the surrounding daylight. Two smaller displaced photophores, one pointing into each eye of the hatchetfish, also ensure that the counter-illumination has the same intensity as the daylight. By adjusting the intensity of bioluminescence produced by these photophores so that it matches the intensity of down-welling daylight, the eyes are able automatically to adjust the intensity of the counter-illumination at different depths, a most extraordinary adaptation.

A marvellous 'misuse' of counter-illumination has been discovered in the cookie-cutter shark *Isistius brasiliensis* (Widder, 1998). This shark has a ventral covering of

photophores that camouflages almost all of its body. The only exception is a small pigmented band located beneath the jaw, a region that is bounded on either side by ventrally directed bioluminescence. This band creates a small but conspicuous silhouette that can be seen from below, of just the shape and size most attractive to predators. Instead of encountering a poorly camouflaged prey, the hapless attacker becomes a tasty meal in itself.

(2) Adaptations for increased sensitivity in deep-sea fishes

In a previous section we saw how the intensity and scattering of light in the ocean, and the intrinsic noisiness of photoreceptors, both set a serious limit to how well marine animals can see. We also saw how various anatomical features of eyes, such as the pupil size, the receptive field width and the photoreceptor volume, might be manipulated to improve sensitivity to an extended scene (equation 1) or to a point-like bioluminescent flash (equation 6). In the dimly lit mesopelagic zone, such manipulations are commonplace, and it is to these fascinating adaptations we turn next.

Ever since the beginning of the last century, the creatures of the mesopelagic zone have been the subjects of intense study and genuine wonder. Early investigators such as Chun, Brauer and Franz, who participated in many of the groundbreaking cruises of research vessels such as the *Challenger*, *Albatross*, *Michael Sars* and *Valdivia*, were the first to describe the eyes of mesopelagic deep-sea fishes and to notice their adaptations for vision in dim light. Later work – especially by Marshall, Munk, Locket and Collin – improved and quantified these early descriptions and this now provides much of our current view of how these eyes have evolved for the deep-sea environment. We will only summarise the highlights, but for a definitive treatment, the following reviews are recommended: Marshall (1954, 1971), Locket (1977), Munk (1980), Collin (1997) and Warrant, Collin & Locket (2003).

(a) Optical adaptations

If they are anything like their freshwater relatives, the eyes of mesopelagic fishes are likely to have ocular media that are remarkably clear, transmitting a greater proportion of the incident light than those of terrestrial eyes, including the eyes of man (Douglas & McGuigan, 1989). Mesopelagic eyes also tend to be large, and most fish species have a sizeable proportion of their brain devoted to vision (Wagner, 2001 *b*). As we have seen, larger eyes with larger pupils can capture more light (equation 1). Whilst no quantitative data exist, this fact is roughly reflected in the eyes of fishes (Marshall, 1979): deeper in the mesopelagic zone eyes tend to become larger relative to the size of their owners, although there are many exceptions. Upon reaching the bathypelagic zone, where daylight is absent, the trend reverses. Below 1000 m eyes tend to become smaller again, although with one important qualification: pupil size relative to eye size tends to become greater (Marshall, 1954; Munk & Frederiksen, 1974), which has important implications for detecting bioluminescent point sources. However, despite the tendency

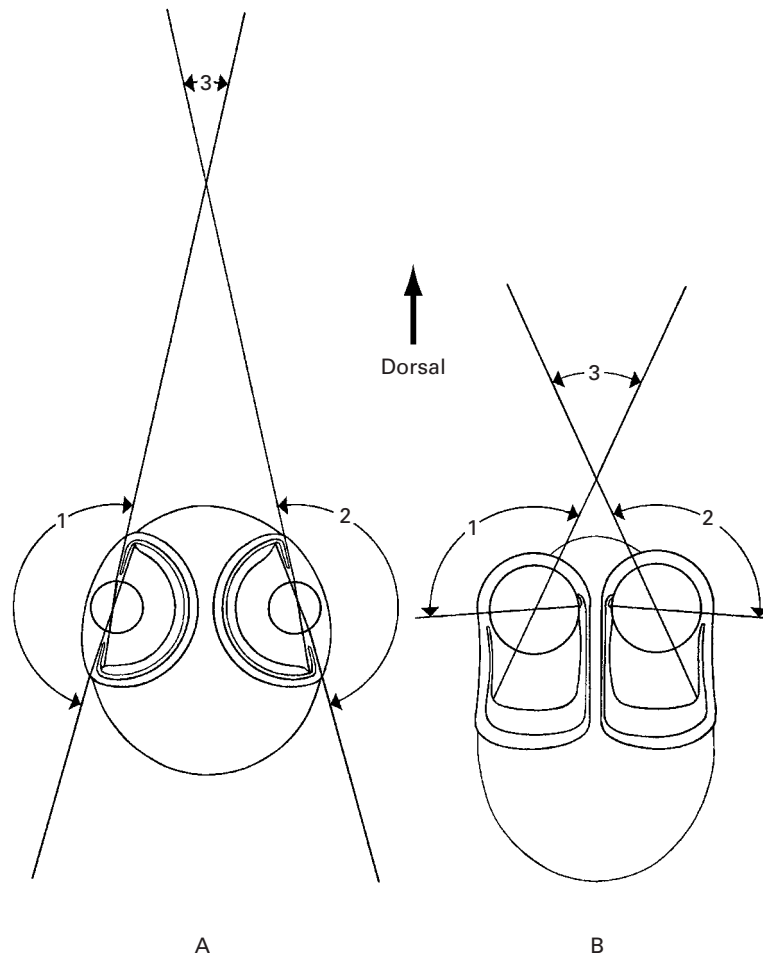


Fig. 5. The two major eye designs of mesopelagic deep-sea fishes (from Warrant *et al.*, 2003). (A) The typical form. (B) The dorsally directed tubular form. 1, visual field of left eye; 2, visual field of right eye; 3, binocular visual field. Adapted from Munk (1980).

for smaller eyes below 1000 m there are again some rather notable exceptions, as we shall see later.

The eyes of mesopelagic fishes occur in one of two main forms (Fig. 5). Munk (1980) refers to one type as the 'typical' form (Fig. 5A): the eyes are placed laterally on the head and have large fields of view with a restricted binocular overlap (as found in most shallow-water fishes). The second form, referred to as 'tubular', is mostly found in fishes from 11 families inhabiting the lower mesopelagic during the day (Munk, 1966, 1980; Collin, Hoskins & Partridge, 1997; Fig. 5B). Tubular eyes are, as their name suggests, tubular in shape, having a large distal spherical lens that focuses a sharp image onto the main retina that lines the weakly concave base of the eye. The tubular shape, which provides good coverage of a small field, severely restricts the main retina's field of view (which is typically less than 50° wide), and the placement of the eyes on the head reflects the importance of the particular direction in which they are pointed. Lie-in-wait predators, such as the bigfin pearleye *Scopelarchus michaelisarsii* (Collin *et al.*, 1998) and hatchetfishes (Fig. 6; Collin *et al.*, 1997), that search for silhouetted prey in the dim down-welling daylight above them, have their

tubular eyes directed dorsally. Fishes such as the telescope fish *Gigantura chuni*, that chase prey swimming directly ahead, have their tubular eyes directed frontally. Some authors have suggested that fishes like *Gigantura chuni* may even orient vertically in the ocean so that the tubular eyes are directed dorsally (Marshall, 1979, p. 387; Ellis, 1996, p. 258).

Despite their narrow fields of view, tubular eyes are very sensitive and, as we shall see below, some are also capable of high resolution. Their large lenses fill the distal half of the eye and the main retina is located where one would expect according to Matthiessen's ratio, with the focal length approximately 2.5 times the radius of the lens (Fig. 6; Collin, 1997; Collin *et al.*, 1997). The full diameter of the lens is usually exposed through the pupil giving maximum light capture along the axis of vision.

Another important contribution to visual sensitivity is the extensive binocular overlap in the visual fields of the two eyes (Munk, 1980). Because both eyes effectively view the same region of space, they collect double the number of photons that would have been collected by a single eye. Stereoscopic calculation of object distance – based on the slight disparity between images falling on the two

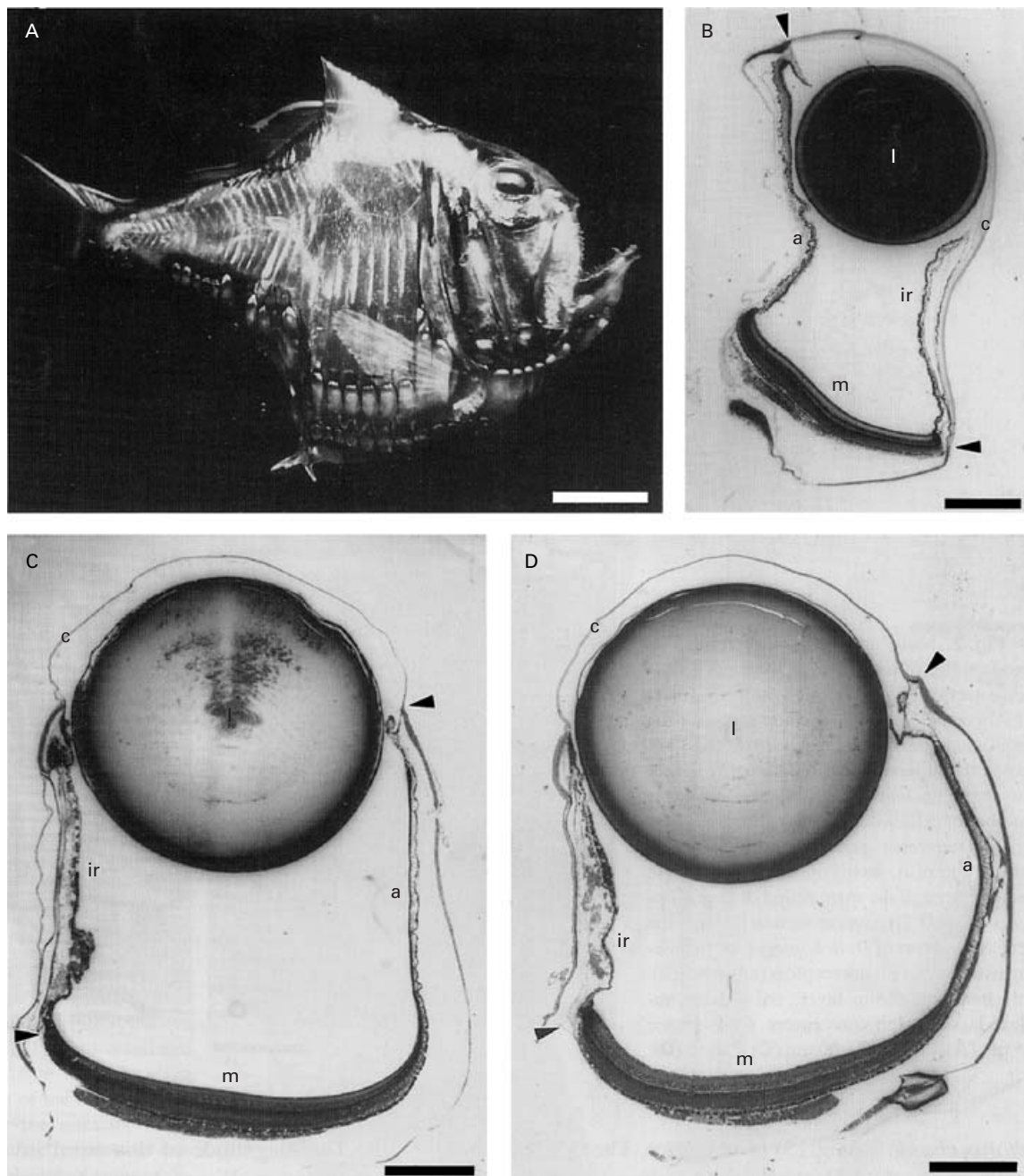


Fig. 6. The dorsally directed tubular eyes of hatchetfishes. (A) The hatchetfish *Argyropelecus aculeatus* showing the dorsally placed tubular eyes and the ventral photophores. (B–D) Transverse sections through the tubular eyes of *A. hemigymnus* (B), *Opisthoproctus soleatus* (C) and *O. grimaldii* (D), showing the main retina (m), the accessory retina (a), the spherical lens (l), and the iris (ir). The cornea (c) extends between the arrowheads. Scale bars: 10 mm (A), 0.5 mm (B–D). From Collin *et al.* (1997).

retinae – also requires binocular vision, an obvious benefit for a predatory deep-sea fish that needs to assess the range of potential prey. Despite these benefits, the narrow visual fields of the main retinæ of tubular eyes severely mask potential dangers, or even food sources, lurking in unseen parts of the fish's immediate surroundings. This problem has been overcome by several remarkable adaptations that extend the visual field of the tubular eye.

The first of these is the presence of a second 'accessory retina' lining the wall of the tubular eye (a in Fig. 6B–D). Even though located far too close to the lens to receive a focused image, this accessory retina nevertheless receives light signals that originate near the side of the fish (Fig. 7A), effectively extending the visual field of the tubular eye by up to 70° laterally. A movement or a bioluminescent flash would be sufficient to trigger the photoreceptors of the

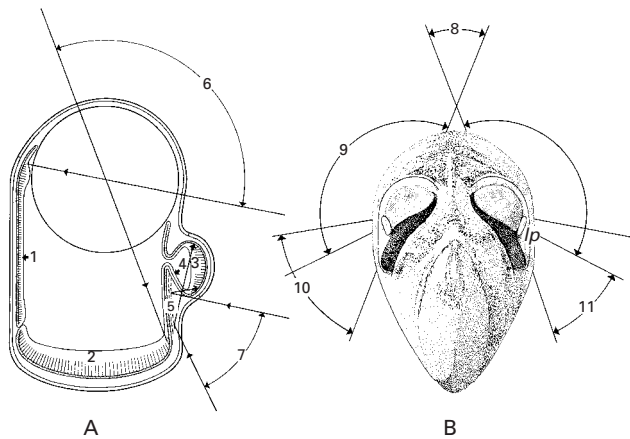


Fig. 7. The visual fields of dorsal tubular eyes, retinal diverticuli and lens pads (from Warrant *et al.*, 2003). (A) A dorsal tubular eye with a laterally placed retinal diverticulum. 1, accessory retina; 2, main retina; 3, retina of the retinal diverticulum; 4, epidermal window; 5, reflective sheet of guanine crystals; 6, the eye's visual field; 7, the retinal diverticulum's visual field. (B) Frontal view of the head of a scopolarchid showing the visual fields of the two eyes. 8, dorsal binocular visual field; 9, visual field of the right eye; 10, total visual field for light reaching the accessory retina through the lens pad (*lp*); 11, ventral extension of the visual field provided by the lens pad. Adapted from Munk (1980).

accessory retina, thus alerting the fish to the fact that it was not alone. Even greater extensions of the receptive field, for much the same purpose, are provided by two other specialised adaptations: 'retinal diverticuli' and 'lens pads' (Percy, Meyer & Munk, 1965; Locket, 1977, 2000; Munk, 1980). The small eye-like retinal diverticulum bulges outwards from the lateral side of some tubular eyes, just proximal to the lens (Fig. 7A). Light originating from the side of the fish, and up to 60° ventral, can be caught by the slender photoreceptors of the diverticulum. Incident light is reflected from an appropriately placed sheet of shiny guanine crystals that are embedded in the iris, and reaches the photoreceptors after passing through a clear epidermal window (Fig. 7A). In one extreme case – *Bathylychnops exilis* – the retinal diverticulum has developed into a separate ventrally pointing eye with its own lens (Percy *et al.*, 1965; Munk, 1966). This little eye presumably has much better spatial resolution than found in the usual accessory retina described above (which receives unfocused light).

Lens pads are common in scopolarchids (*lp* in Fig. 7B). This structure, formed of lamellae derived from corneal endothelial cells, is located in the same position that a retinal diverticulum would have been: on the lateral side of the tubular eye, just lateral to the lens. Locket (1977) has observed the optical structure of the lens pad and concludes that it is a transparent light-guiding structure that directs light, originating from up to 70° ventral, to the dorsal-most part of the accessory retina (Fig. 7B). In the scopolarchid *Benthalbella infans* – and probably in other scopolarchids – the lens pad can also disperse broad-spectrum light into its

component wavelengths, an ability that may aid in the detection of bioluminescent counter-illumination (Locket, 2000).

Compared to tubular eyes, those of 'typical' form tend to have very large lateral receptive fields, which easily survey a good deal of a fish's surroundings. One potential problem arises frontally, the direction a forward swimming fish is most likely to encounter and pursue prey: lateral receptive fields restrict the extent and sensitivity of frontal vision. Frontal binocular overlap – and distance discrimination – is also compromised. This problem has been overcome in many deep-sea fishes by a large 'rostral aphakic gap', a frontal elongation of the pupil far beyond the margin of the lens (Fig. 8A; Munk & Frederiksen, 1974). This, together with sighting grooves along the snout, allows the full diameter of the lens to collect light frontally and to focus it onto the temporal (i.e. posterior) part of the retina (Fig. 8B). Without an aphakic gap, only a fraction of the lens would have been exposed frontally, severely limiting light capture. As we will see, the temporal retina frequently possesses an acute fovea, or an area centralis, a region with densely packed ganglion cells, and the rostral gap ensures that it receives a bright image. However, light incident more laterally has the chance to leak unfocused into the eye through the aphakic gap, contaminating the lateral image. But this price is apparently worth the gain in frontal visual performance. For those deep-sea eyes that need to maximise the amount of light reaching the retina, focused or otherwise, a 'circumlental aphakic gap' is a common adaptation (Fig. 8C; Munk & Frederiksen, 1974). This is a pupil larger than the lens in all directions (not just rostrally) and the intervening gap surrounding the lens tends to be larger in fishes living deeper. This allows the full aperture of the lens to be exposed for light capture over a substantial part of the eye's visual field, thus maximising image brightness (Fig. 8B, D). However, unfocused light can also leak through the gap into the eye and contaminate almost the entire retina with an image-degrading background haze, although this will be worse for extended fields of light than for point sources of bioluminescence on a dark background. But for an eye starved of photons, the boost in sensitivity provided by a circumlental gap could mean the difference between detecting a weak stimulus and remaining ignorant of it, despite the losses in resolution.

Once light reaches the retina, the eyes of many mesopelagic fishes have a further optical adaptation that maximises its absorption: a reflective layer – or tapetum – that lies behind the retina. In deep-sea teleosts, the tapetum is constructed from stacks of needles, or oriented crystals of guanine, housed within the retinal pigment epithelium, or in some species within the choroid (Locket, 1977; Collin, 1997; Douglas, Partridge & Marshall, 1998*b*). By reflecting light back through the retina, the tapetum allows a second chance for absorption of light that has not been absorbed during its first passage through the rods, thus effectively doubling the lengths of the outer segments. Despite this improvement in sensitivity, the unconstrained reflection provided by a flat tapetum can degrade spatial resolution (Munk, 1980; Nicol, 1989; Warrant & McIntyre, 1991). An exception is the choroidal tapeta of sharks: guanine

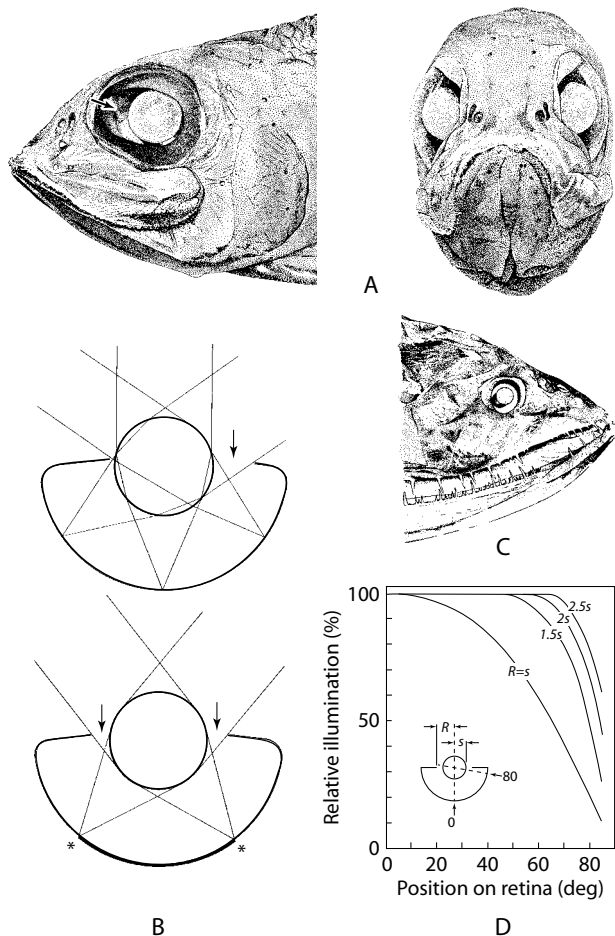


Fig. 8. Aphakic gaps in the eyes of deep-sea fishes (from Warrant *et al.*, 2003). (A) A rostral aphakic gap (arrow) in the eye of *Bathytroctes microlepis*. Together with sighting grooves in the snout, the rostral aphakic gaps entirely expose the lens of each eye in the frontal visual field. The temporally placed foveae that view the same frontal field are then assured of maximum light capture. From Munk (1980). (B) The function of rostral (upper) and circumlental (lower) aphakic gaps (arrows). A small circumlental gap allows the retinal area delimited by the stars to be illuminated by the full aperture of the lens. A rostral gap allows full illumination of only the central and temporal areas of the retina. Unfortunately, the nasal areas of the retina also receive unfocused light. Adapted from Locket (1977). (C) Circumlental aphakic gaps surround the entire lens, as shown here in *Gonostoma bathyphilum*. From Munk & Frederiksen (1974). (D) The effect of circular circumlental aphakic gaps on illumination at different angular positions on the retina. As the radius of the gap (R) increases relative to the radius of the lens (s), the illumination of the retina increases, especially in the periphery. Re-drawn from Munk (1980).

plates aligned with the light path improve sensitivity without appreciable loss in resolution (Walls, 1942). Due to their pigmentation or physical structure, the tapeta of many deep-sea fishes are wavelength selective, typically being most reflective from the ultraviolet to the green regions of the

spectrum with a distinct reflection peak in the blue (Douglas *et al.*, 1998*b*). This is hardly a surprise, considering that these are the most common wavelengths in the deep sea, and that the rods of deep-sea fishes are maximally sensitive to light within the same range (see below). One interesting case is the lantern fish *Notoscopelus resplendens*, which has a divided tapetum that appears perfectly matched to the mesopelagic light environment (Douglas *et al.*, 1998*a*). One section, having a blue reflection peak at 470 nm, is positioned in the ventral retina where it reflects the dominantly blue down-welling daylight originating in the dorsal field of view. The other section has a violet reflection peak at 390 nm, and is positioned in the dorsal retina. This reflectance peak is well adapted for reflecting the violet up-welling light that is found in the shallower depths of the ocean down to 200 m. For *N. resplendens* this would only be a useful at night, following its daily upward migration to depths of 100–300 m. During the day, it is only found in the lower mesopelagic zone (Hulley, 1984). Presumably the photoreceptors in each section of the *N. resplendens* retina have visual pigments that are maximally absorbent to the same wavelength peaks.

(b) Neural adaptations: the properties of individual rods

The optical adaptations we have described so far all improve sensitivity by making the aperture through which light reaches the retina larger, a benefit for both point- and extended source detection. This is equivalent to increasing A in equations (1–6). But this is not the only strategy available. For extended source detection (equation 1), a larger visual channel receptive field ($\pi d^2/4f^2$ steradians), or a longer (l) and more absorbent (k) photoreceptor will also improve sensitivity. Deep-sea fishes are highly specialised in these respects as well.

The retinæ of deep-sea fishes tend to be exclusively constructed of tightly packed rod photoreceptors. Rods, as opposed to cones, are the photoreceptor class responsible for nocturnal vision in terrestrial vertebrates, so their employment for deep-sea vision comes as little surprise. A typical deep-sea rod outer segment is long, over 100 μm (compared to just 26 μm in humans), and has an absorption coefficient k at least twice that (e.g. $0.064 \mu\text{m}^{-1}$; Partridge *et al.*, 1989) of rods in animals from brighter habitats (Warrant & Nilsson, 1998). The outer segments also tend to have visual pigments (rhodopsin or porphyropsin) whose spectral absorption peaks typically match the blue–green wavelengths most common in the deep sea (from daylight and bioluminescence). In fact approximately 87% of all visual pigments so far investigated in deep-sea fishes have a peak absorption wavelength (λ_{max}) in the range 468–494 nm (Fig. 9A; Douglas *et al.*, 1998*b*; Douglas, Hunt & Bowmaker, 2003), a match that apparently ensures maximum sensitivity to the available light, especially down-welling daylight at 475 nm. However, this conclusion is somewhat simplistic. If one takes careful account of the spectrum of down-welling daylight, the full absorption spectrum of the visual pigment, and the attenuation coefficient of water, it is possible to calculate the optimal λ_{max} value for detecting daylight at mesopelagic depths (Douglas *et al.*, 1998*b*, 2003). For the clearest ocean water (Jerlov type I; Fig. 1), the optimal λ_{max}

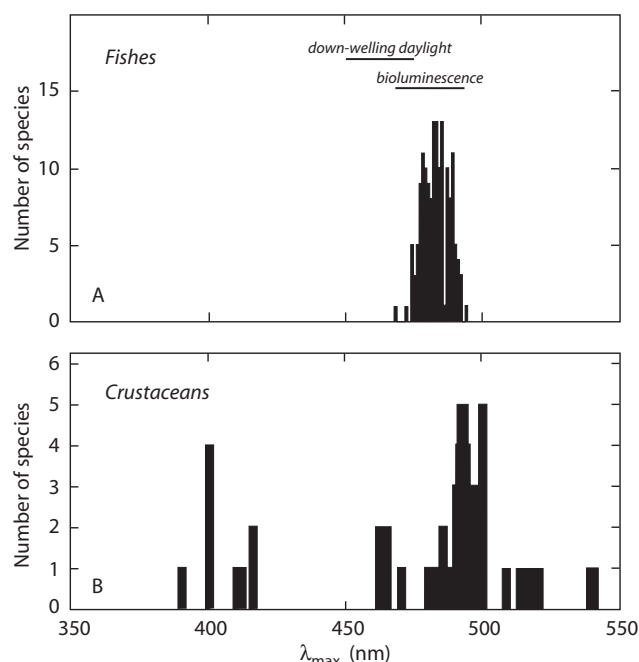


Fig. 9. The spectral distribution of peak absorption wavelengths (λ_{\max}) in visual pigments from 175 species of deep-sea fishes (A), and several species of decapod, mysid and euphausiid crustaceans (B). The horizontal bars in (A) show the range of fish λ_{\max} values predicted to confer maximum sensitivity to down-welling daylight and fish bioluminescence. In crustaceans (B), visual pigments from retinula cells 1–7 (R1–7) have λ_{\max} in the range 480–540 nm. Some species also possess a second UV-violet pigment in retinula cell 8 (R8), with λ_{\max} around 400 nm. (A) adapted from Douglas *et al.* (1998*b*), (B) adapted from Marshall *et al.* (1999).

turns out to be less than 474 nm, implying that most visual pigments are actually poorly adapted for maximising sensitivity to down-welling daylight, at least in these very clearest waters (Douglas *et al.*, 1998*b*, 2003). The same type of calculation predicts a different result for bioluminescence: the optimal λ_{\max} values for detecting mesopelagic bioluminescence almost exactly overlap the range of λ_{\max} values measured in the visual pigments (Fig. 9A). This result suggests that deep-sea visual pigments are actually better adapted to improving sensitivity to bioluminescence. However, many other factors – including minimising dark noise, the effects of tremendous pressure (70 atmospheres at 700 m: Marshall, 1954), and phylogenetic constraints – may all contribute to the exact placement of λ_{\max} values (Douglas *et al.*, 1998*b*, 2003).

Almost all investigated deep-sea fishes (approximately 89%) possess a single visual pigment (Douglas *et al.*, 1998*b*), as one might predict for a near-monochromatic world. However, the other 11% represent a significant exception to the rule, with many species possessing two pigments that have λ_{\max} values in the ‘normal’ range of 468–494 nm. Some scopolarchids even have three pigments, with λ_{\max} values spread out over a somewhat greater range in the blue-green (Partridge, Archer & van Oostrum, 1992). Two

or more visual pigments have the potential to bestow wavelength discrimination, an ability that requires opponent interactions between the different rod classes, and the relevant retinal circuitry to mediate it. No one yet knows whether these interactions and circuitry actually exist, but if they do, some deep-sea fishes could have the ability to make colour discriminations. This might prove particularly useful for those species having two visual pigments, one of which has greatest sensitivity to the down-welling daylight, the other to bioluminescence. Wavelength discrimination might allow such fishes to easily discern these two similarly coloured sources of light, thus providing a mechanism for breaking the less than perfect bioluminescent camouflage of organisms swimming above them (Douglas *et al.*, 1998*b*). We discussed this type of camouflage – produced by photophores on the ventral body surface – in Section VI.1. Wavelength discrimination, finely tuned in the blue-green part of the spectrum, might easily expose camouflaged prey. We will return to this fascinating topic later, when we explore adaptations for breaking mesopelagic camouflage.

One extraordinary group of deep-sea fishes – three genera of dragon fishes from the family Stomiidae – have at least three visual pigments, all of them shifted to longer wavelengths (Partridge & Douglas, 1995; Douglas *et al.*, 1998*a, b*; Douglas, Mullineaux & Partridge, 2000). One of these pigments is most sensitive to orange light, and there is even thought to be a fourth sensitive to far-red light. These visual pigments have evolved to allow dragon fishes to see their own bioluminescence. In addition to a battery of ventral photophores, they also possess two other specialised light organs: a postorbital photophore producing regular blue-green bioluminescence, and a suborbital photophore producing a very unusual far-red bioluminescence that peaks sharply at wavelengths beyond 700 nm (Denton *et al.*, 1970, 1985). This unique red bioluminescence would be invisible to other deep-sea animals, thus providing a ‘private waveband’ which dragon fishes could use to signal secretly to one another (and avoid discovery by predators) or to covertly illuminate their prey. These long wavelengths are rapidly absorbed in water (Fig. 1B), and this limits the useful range of far-red bioluminescence to less than 2 m (Partridge & Douglas, 1995). In one species, *Malacosteus niger*, there are two visual pigments with λ_{\max} values of 515 nm and 542 nm. A third pigment – remarkably based on chlorophyll-derived compounds originating in their copepod prey – is most absorbent at 670 nm (Douglas *et al.*, 1998*a*, 2000, 2003). This pigment is thought to act as a photosensitiser that absorbs red bioluminescence and somehow transfers the photon energy to the shorter wavelength pigments, which then isomerise. In addition, the eyes of *Malacosteus niger* have tapeta that selectively reflect red light, an adaptation that further improves sensitivity to red bioluminescence (Locket, 1977; Douglas *et al.*, 1998*b*).

(c) Neural adaptations: rods in layers and groups

A deep-sea fish with rods 100 μm long (effectively 200 μm with a tapetum), absorbing light with $k = 0.064 \mu\text{m}^{-1}$ (Partridge *et al.*, 1989), will absorb a fraction ($1 - e^{-0.064 \times 200} = 0.999997$) of the monochromatic light

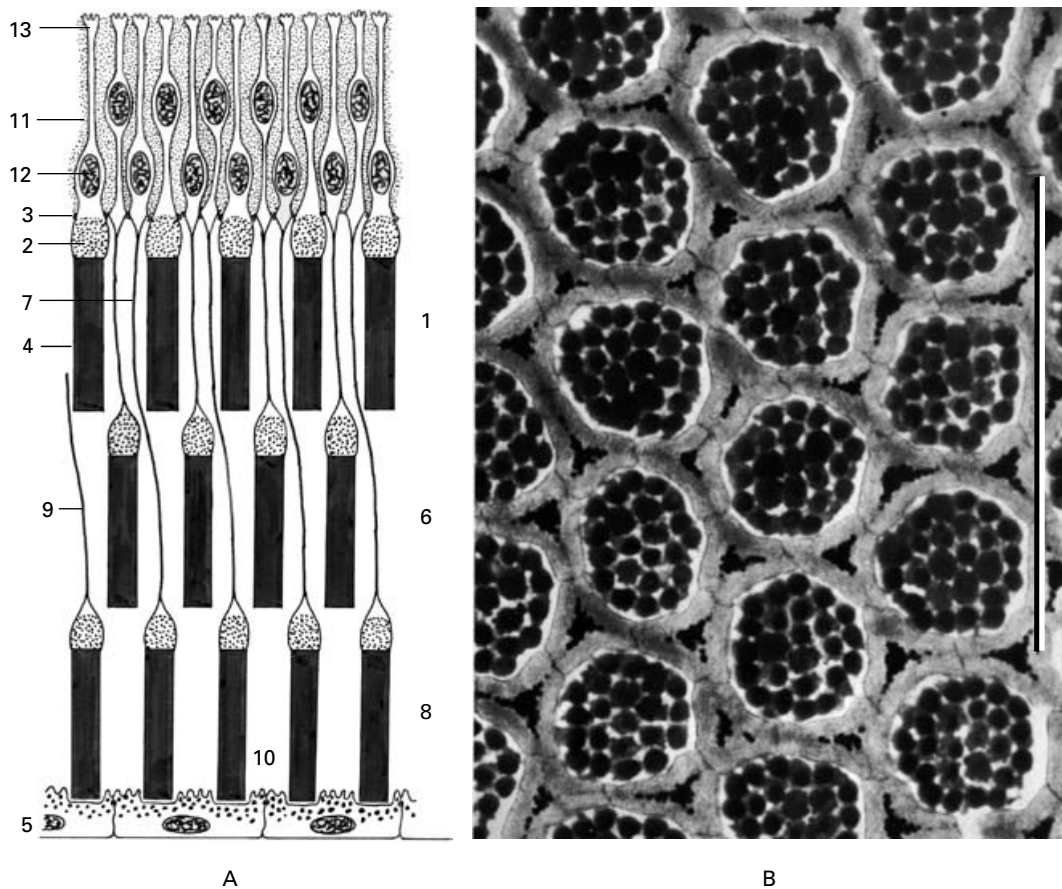


Fig. 10. Retinal adaptations for increased sensitivity to extended sources in deep-sea fishes (from Warrant *et al.*, 2003). (A) A multibank retina consisting of three banks (1, 6 and 8). 2, ellipsoid; 3, outer limiting membrane; 4, outer segment; 5, pigment epithelium; 7, 9, filamentous myoids; 10, ventricular space; 11, radial fibre cytoplasm; 12, rod nuclei; 13, synaptic spherules. (B) The grouped retina of *Scopelarchus guntheri*, sectioned tangentially at the level of the inner-outer segment junctions. Scale bar = 50 μm . From Locket (1977).

that is incident upon them (equation 1). This is effectively all of the light! Strangely, despite this, deep-sea fishes have yet another adaptation that has been interpreted as improving sensitivity: instead of a single layer (or bank) of rods in the retina, they are often stacked several layers deep (Fig. 10A). These are usually well ordered, but in some cases the layers are scattered in depth without apparent order. In some multibank retinæ there are six layers of rods, and such an arrangement would increase the path length for light absorption by a factor of six. The stacks are most numerous in the most important parts of the retina, such as in temporal foveae that are responsible for sharp frontal binocular vision. There is growing evidence that not all layers are functional (Locket, 1980; Collin, 1997), and that the actual optical path length might therefore be shorter than one might first suppose. In at least one case, that of *Chauliodus sloani*, it has been shown that the fish adds layers as it grows (Locket, 1980). The layers of rods further from the incident light are older and may well have been replaced by newer functional layers during a process of regeneration. Could it be that the receptors of a layer have a finite functional life under the extreme conditions of the ocean deep, and are

replaced by a new layer periodically? Why the old receptors are not removed is not clear: in most shallow or terrestrial animals there is a constant turnover of outer segment material.

Another intriguing explanation for multibank retinæ, first proposed by Denton & Locket (1989), is that the more vitread layers could act as spectral filters for more sclerad layers. Even with a single visual pigment throughout all layers, this filtering might be sufficient to change the spectral sensitivities of layers more sclerad. This could endow the retina with the ability to make simple wavelength discriminations, particularly in the blue-green range that encompasses daylight and bioluminescence. If two visual pigments are present, each confined to different layers (as indeed seems to be the case in some species: see Denton, 1990), then the possibilities for this type of wavelength discrimination are even greater. Such a strategy may be of benefit in breaking the camouflage of fishes with photophores.

The prize for the most extreme multi-banked retina goes to the alepocephalid *Bajacalifornia drakei*, which has two ill-defined banks in the periphery, and no less than 28 layers of

rods in its deep temporal foveae (Locket, 1985). The rods are only approximately $27\text{ }\mu\text{m}$ long, but the 28 layers ensure an optical path length l of $750\text{ }\mu\text{m}$. With $k=0.064\text{ }\mu\text{m}^{-1}$ the 28 banks again absorb essentially all the monochromatic light that is incident upon them. This would have been the situation had there been only three or four layers present, so why are there 28 (assuming all are functional)? One possibility is that *Bajacalifornia drakei* is more interested in looking at broader spectrum bioluminescence (Lythgoe, 1972; Herring, 1983), rather than the blue monochromatic space light. The fraction of incident light absorbed from such sources is better described by $kl/(2.3+kl)$ (Warrant & Nilsson, 1998). In this case, the fraction is 0.95 (95% absorption). Had there been only four layers, absorption would have been 74%, and this might be unacceptably low in the light-famished deep sea.

The final adaptation for increasing sensitivity is to widen the receptive fields of the visual channels (equation 1). Wider receptive fields capture more light, but only at the expense of spatial resolution. Nevertheless, the drive for photons in dim light has led to adaptations that have overcome the narrow receptive fields imposed by the slender rods, which are typically only 2 or $3\text{ }\mu\text{m}$ wide. One of the best-studied adaptations is found in the 'grouped retinæ' of notosudids, evermannellids and scopolarchids. In the tubular-eyed scopolarchids, groups of more than 20 rod outer segments are bundled into round cups of retinal epithelium cells filled with reflective guanine crystals (Fig. 10B; Locket, 1971, 1977, 1999; Collin *et al.*, 1998). These reflective cups optically isolate the receptor groups from each other, effectively turning the rod bundle into a kind of 'macroreceptor', with the outer segments in close contact, so that light entering the cup is trapped and shared by all of them. This will result in a much wider – and presumably more sensitive – receptive field than achievable by a single rod. In *Scopolarchus guntheri*, 23 rods, each approximately $2.5\text{ }\mu\text{m}$ wide, fill a cup that is $18\text{ }\mu\text{m}$ wide (Locket, 1971, 1977), coarsening spatial resolution from 0.14° between rods, to approximately 1° between groups. However, the new macroreceptor has a receptive field over seven times wider than a rod, increasing sensitivity by 50 times. Elsewhere in the main retina of *Scopolarchus guntheri* the rods are organised as a single uniform bank.

The related *Benthalbella infans* shows a further adaptation. In some areas of the retina there is a uniform population of rods located in front of a second population of grouped rods, the latter segregated by a reflecting tapetum as in *Scopolarchus guntheri*. Here there is the possibility for an image being resolved in the frontal, ungrouped, population, while light penetrating that layer will be further analysed at the coarser resolution of the groups.

The evermannellid fishes, also with tubular eyes, show grouping of a different kind in their main retina. Radial sections of this retina show areas of uniform single rods approximately $1.2\text{ }\mu\text{m}$ in diameter, but not closely packed. Other areas appear 'untidy' in radial sections, and contain a thick and densely packed outer nuclear layer. The nature of the outer segments is not clear from such radial sections, but becomes so in tangential sections. These sections show that narrow outer segments are present in small groups of 2–6.

These groups will function differently to those of the scopolarchids, due to their different dimensions. The resolution afforded by the single rods will depend on their size and separation, and on whether the eye conforms to Matthiessen's ratio, which inspection suggests that it does. A figure of approximately 4 min of arc is obtained. The individual outer segments of the small groups are only approximately $0.7\text{ }\mu\text{m}$ wide, and the groups themselves are not much wider than this at approximately $1.3\text{ }\mu\text{m}$. At this size each group will behave as a single entity optically, with resolution corresponding to their size and separation. The number of synaptic outputs will be that of the number of rods in the group, leading to neural convergence. If these conclusions are correct, the fish has produced a nice compromise between resolution and sensitivity.

Spatial summation of rods need not be as obvious as physically grouping them in a reflective pigment cup. Via the bipolar cells, rods in all vertebrate retinæ converge in large numbers onto single ganglion cells, and the size of the converging rod pool sets the potential sensitivity of the receiving ganglion cell and the local visual resolution (Collin, 1999). A smaller rod pool builds a smaller and less sensitive ganglion cell receptive field, and the density profile of ganglion cells across a retina reveals the trade-off between spatial resolution on the one hand, and sensitivity to an extended source on the other. Denser packing of ganglion cells indicates a region of higher resolution where spatial summation – and thus sensitivity to a dim extended source – has been sacrificed. As we shall see below, many deep-sea fishes take this to an extreme, possessing highly specialised retinæ with areas of excellent resolution. Many others tip the scale in the opposite direction, and favour extensive rod summation and high sensitivity. These fishes have an unspecialised retina with regard to ganglion cells, with rather uniform distribution and lower density. Good examples include lower mesopelagic lantern fishes in the genus *Lampanyctus* (Collin & Partridge, 1996; Wagner *et al.*, 1998). These have a uniformly low density of ganglion cells, and presumably high rod convergence, throughout the retina. With only 1000–3000 ganglion cells mm^{-2} , visual acuity is no better than approximately 0.5° , much lower than in other deep-sea fishes with specialised retinæ (see below).

(d) Case example: the sensitivity of a lantern fish eye

Our discussions throughout this section now allow us to calculate the sensitivity of a deep-sea fish eye to an extended field of light. Let us take the lantern fish *Lampanyctus macdonaldi* as an example, and assume all light incident on the photoreceptors is absorbed. In *L. macdonaldi*, the pupil diameter A is $2500\text{ }\mu\text{m}$, the focal length f is $1.25A = 3125\text{ }\mu\text{m}$ (Matthiessen's ratio), and the diameter of a ganglion cell receptive field is $25\text{ }\mu\text{m}$ (assuming 2000 cells mm^{-2}). From equation (1), the sensitivity S of the eye to an extended source is then $247\text{ }\mu\text{m}^2\text{ sr}$, a very high value for a vertebrate eye, in fact approximately 100 times more sensitive than for a nocturnal toad (Warrant & Nilsson, 1998). The eyes of deep-sea fishes are up to 120 times more sensitive to an extended scene than the human eye (Munk, 1980; Denton, 1990).

(3) Adaptations for increased sensitivity in crustaceans and cephalopods

For sensitive eye designs, the invertebrates cannot be beaten. The superposition eyes, concave mirror eyes and even apposition eyes of many mesopelagic crustaceans have adaptations that endow them with great sensitivity to both extended and point-source light. Some animals, like the mesopelagic cephalopods, increase light capture simply by having very large eyes with wide pupils.

(a) Optical adaptations

With respect to sensitivity to a dim extended source, the compound eyes and concave mirror eyes of invertebrates have one important advantage over the camera eyes of fishes: the size of the pupil aperture (A), relative to the eye's focal length (f), can be made very large. That is to say, an invertebrate eye's 'F-number' (f/A) can be very low. F-numbers are often used to describe the light-gathering capacities of photographic lenses and a lower F-number means a brighter image. In a fish eye, the F-number is constrained by the optics to a value of around 1.25, as specified by Matthiessen's principle: $f=1.25A$ (we have assumed here that the pupil is the same diameter as the lens). This is probably more or less similar for all fishes. F-numbers in deep-sea crustaceans can be much lower than this, and in one extreme case, the bathypelagic ostracod *Gigantocypris mülleri*, it reaches a record low value of 0.25 (Land, 1981a)! However, just as in fishes, the eyes of invertebrates also increase sensitivity to the dim extended space light by employing reflective tapeta (for a review, see Douglas & Marshall, 1999). These lie proximal to the photoreceptors and double the path length for light absorption in the retina, but generally at the expense of spatial resolution (Warrant & McIntyre, 1991).

As in fishes, larger eyes with larger pupils have greater sensitivity to light. In this respect, perhaps the most sensitive eye of all – and unquestionably the largest – is owned by a cephalopod, the giant deep-sea squid *Architeuthis dux*. One specimen captured off the Irish coast in the late 19th century is reported to have had a camera-type eye measuring 37 cm across (Land, 1981a). Although the pupil diameter was not noted, it could easily have been 20 cm wide. Such enormous sensitivity might endow them with formidable visual powers at great depths, and would certainly allow them to see prey long before being detected themselves. Many other cephalopods, of more modest size, also have large eyes relative to body length. *Octopus* sp. has a sensitivity of around $4 \mu\text{m}^2 \text{sr}$ which does not sound extremely high until one realises that it is achieved while maintaining a spatial resolution approaching that of the much less sensitive human eye (Land, 1981a).

(b) Neural adaptations

Just as in mesopelagic fishes, mesopelagic crustaceans have visual pigments with λ_{max} values located in the blue–green part of the spectrum, although over a somewhat larger wavelength range (Fig. 9B; Marshall, Kent & Cronin, 1999; Cronin, Marshall & Frank, 2003). Those mesopelagic

crustaceans that have so far been investigated have a visual pigment with λ_{max} in the range 480–540 nm, and this is typically located in retinula cells 1–7 (R1–7). Some species also possess a second UV-violet pigment in retinula cell 8 (R8), with λ_{max} around 400 nm. Interestingly, this pair of pigments is typical of crustaceans from all depths, and does not seem to be a specialisation for the mesopelagic zone (Marshall *et al.*, 1999). The λ_{max} values of the blue–green pigments (average 493 nm) are longer than expected for maximum sensitivity to the down-welling daylight (475 nm). This is quite similar to the situation we saw earlier in mesopelagic fishes (Fig. 9A). Just as with fishes, it may be the case that the blue–green visual pigments of mesopelagic crustaceans have evolved for increased sensitivity to bioluminescence, rather than for the dim down-welling daylight. But again, the exact placement of λ_{max} values may depend on many factors, including phylogeny and the extreme pressures of the deep sea (Douglas *et al.*, 1998b).

Most cephalopods that have been investigated have a single visual pigment with a λ_{max} value in the range 470–500 nm (Messenger, 1981; Seidou *et al.*, 1990). Mesopelagic species have λ_{max} around 470–480 nm, as might be expected for maximum sensitivity to the down-welling daylight. There are some cephalopods, however, that possess two (e.g. the octopus *Japetella* sp. and the squids *Pyroteuthis* sp. and *Pterigoteuthis* sp.), or as many as three (e.g. the squids *Bathyteuthis* sp. and *Watasenia scintillans*), visual pigments (Kito *et al.*, 1992). The best-known example is the remarkable mesopelagic firefly squid *Watasenia scintillans* (Matsui *et al.*, 1988; Michinomae *et al.*, 1994), which has a tiered retina of photoreceptors and three visual pigments ($\lambda_{\text{max}} = 470, 484$ and 500 nm, each based on a different chromophore: A4, A1 and A2, respectively). The 484 nm pigment is found throughout the retina, whereas the other two are found only in the ventral region of the retina. With three pigments present in the ventral retina, the firefly squid has the potential to make complex colour discriminations, which may prove useful in the spring, when it comes to the surface for communal spawning. This activity involves intense bioluminescent displays from a battery of photophores covering the body and tentacles.

Mesopelagic invertebrates can also improve their sensitivity to the dim extended space light by having photoreceptors with wide visual fields that sum photons across space. But as we have mentioned earlier, this is not the only strategy. Photoreceptors struggling to capture light can also have longer exposure times. This is achieved by having slower photoreceptor responses that sum photons over a longer time window. For animals living in the brighter upper levels of the ocean the exposure time – or 'integration time' – can be kept quite short, but in the continuously darker depths, longer and longer exposures would be expected (Warrant, 1999). This prediction is very difficult to test, but Moeller & Case (1994, 1995) have discovered that deep-sea mysids do indeed have very long visual integration times – up to 160 ms – very long for an arthropod. Day-active houseflies *Musca domestica* have integration times more than 20 times shorter. There is also a clear dependence on depth. Marine crustaceans from the upper layers of the mesopelagic zone have two to three times faster

vision than those from the lower layers (Frank, 1999, 2000; Cronin *et al.*, 2003), and this is precisely the trend one would predict.

(c) *Case example: the sensitivity of a mesopelagic crustacean eye*

A very sensitive reflecting superposition eye is that of the mesopelagic shrimp *Oplophorus spinosus*, an animal approximately 5 cm long (Land, 1976, 1981*a*). With a superposition aperture almost 1 mm wide, and gigantic photoreceptors ($32 \times 200 \mu\text{m}$), these eyes attain a very high sensitivity of $3300 \mu\text{m}^2 \text{sr}$. Unfortunately, they probably cannot distinguish point sources closer than 15° apart (Land, 1976), but presumably they do not need to either.

(4) Point source or extended source?

The transition from extended scenes in the upper mesopelagic zone to domination by point-source bioluminescence at greater depths brings with it a change in retinal organisation. Wide pupils and large absorbant photoreceptors improve sensitivity no matter what the source, point or extended (although in fishes, with lenses of constant F-number irrespective of eye size, extended source sensitivity will only improve if the wider pupil exposes more of the lens). By contrast, the wide visual channel receptive field that results from spatial summation (as in unspecialised fish retinae) only improves sensitivity to an extended source. It has no effect on sensitivity to a point source. As we said above, to collect all the light from a point source the receptive field need not be any larger than the point-like image itself. Making the receptive field larger only degrades the eye's ability accurately to localise the point source. Deep-sea animals that need to localise point-source bioluminescent flashes thus tend to have wide pupils and sharp spatial resolution (Warrant, 2000).

The eyes of deep-sea fishes beautifully exemplify this transition from extended to point-source detection (Fig. 11). In the mesopelagic zone, where extended space light and bioluminescent flashes coexist, the retinae of fishes can be adapted to one or both of these light sources. The 'typical' eyes of the deepwater bass *Howella sherborni*, an upper mesopelagic fish living at depths ranging from 25 to 300 m, have rostral aphakic apertures collecting light from the frontal visual field. Its retinal ganglion cell distribution (Fig. 11A) shows a large temporal area of higher resolution – the 'area centralis' – that nearly covers the entire frontal field of view, and analyses it with at least 14 000 ganglion cells mm^{-2} (Collin & Partridge, 1996). Embedded within the area centralis is a deep fovea comprising a multibank retina of 22 rod layers (Best & Nicol, 1978) and up to 24 500 ganglion cells mm^{-2} (Locket, 1992; Collin & Partridge, 1996). This retina is clearly designed to view an extended scene with high resolution, as might be expected of a predator that depends on the surrounding space light to illuminate its prey. Deeper down in the mesopelagic zone, between 450 and 1000 m, point-like bioluminescent flashes begin to dominate. This is the habitat of the platytroctid *Searsia koefoedi*, a fish with an eye design similar to that of *Howella sherborni* but with a very different retina (Fig. 11B).

It too has an increase in ganglion cell density in the temporal retina, even reaching a similar maximum density (approximately 24 000 cells mm^{-2}), but unlike *Howella sherborni*, its region of high resolution is much smaller (Collin & Partridge, 1996). *Searsia koefoedi* has a steep-sided convexiculate fovea that is ideal for detecting and localising point sources (as we will see below when we discuss the eyes of bathypelagic fishes). Another fish living at the same depths as *S. koefoedi* has a retina that is better adapted for detecting the dim extended lower-mesopelagic space light. This is the lantern fish *Lampanyctus macdonaldi*, whose 'unspecialised' but sensitive retina we have discussed already. Other fishes seem to have eyes adapted for both types of sources. The dorsally directed tubular eyes of the bigfin pearleye *Scopelarchus michaelisarsii* have retinal areas devoted separately to point sources and extended sources (Fig. 11C; Locket, 1971, 1977; Collin *et al.*, 1998).

This transition in eye design is clearly seen by plotting the smallest angular separation of ganglion cells as a function of depth for some 20 species of deep-sea fishes (Warrant, 2000, using data given in Wagner *et al.*, 1998). A narrower separation of ganglion cells results in a greater anatomical acuity. Two important features can be seen in the resulting histogram (Fig. 11D). First, the eyes of fishes on average become sharper with depth, with the eyes of bathypelagic fishes being the sharpest, typically having the potential to resolve details subtending just 5 minutes of arc. This is perfect for detecting point-source bioluminescence, the only light source at these depths. Secondly, the variation across species in ganglion cell separation (and thus acuity) is large in the brighter upper levels (Fig. 11D: error bars), but gradually declines with depth, with minimal variation in the bathypelagic zone (separation = 4.8 ± 2.9 arc min). The small variation in the bathypelagic zone is easy to understand: here the only light sources are point sources and the best strategy involves little summation and high acuity. The large variation in the mesopelagic zone reflects its semi-extended nature, with some species adapted to point sources, some to extended sources, and others to both (Warrant, 2000).

(5) Adaptations for the directionality of deep-sea light

The increasingly downward direction of daylight at greater depths (Fig. 1C) has also been a major force in the evolution of aquatic vision. To catch as much of the down-welling light as possible, and to enhance the discrimination of any small object that might be silhouetted against it, many aquatic eyes have evolved narrow, dorsally directed visual fields. The dorsal tubular eyes of deep-sea fishes, like hatchetfishes (Fig. 6) and scopelarchids, are a classic example. Typically, the narrow visual field is matched in the retina by an enhanced spatial resolution.

The main adaptations for the increasing directionality of deep-sea light with depth are seen in the large apposition eyes of hyperiid amphipods, as shown in the elegant studies of Land (1989*a*, 2000). These highly mobile crustaceans can be found at all depths down to 1000 m, with different species being adapted for life and vision at different depths. Surface-living species like *Thamneus* sp., have small eyes

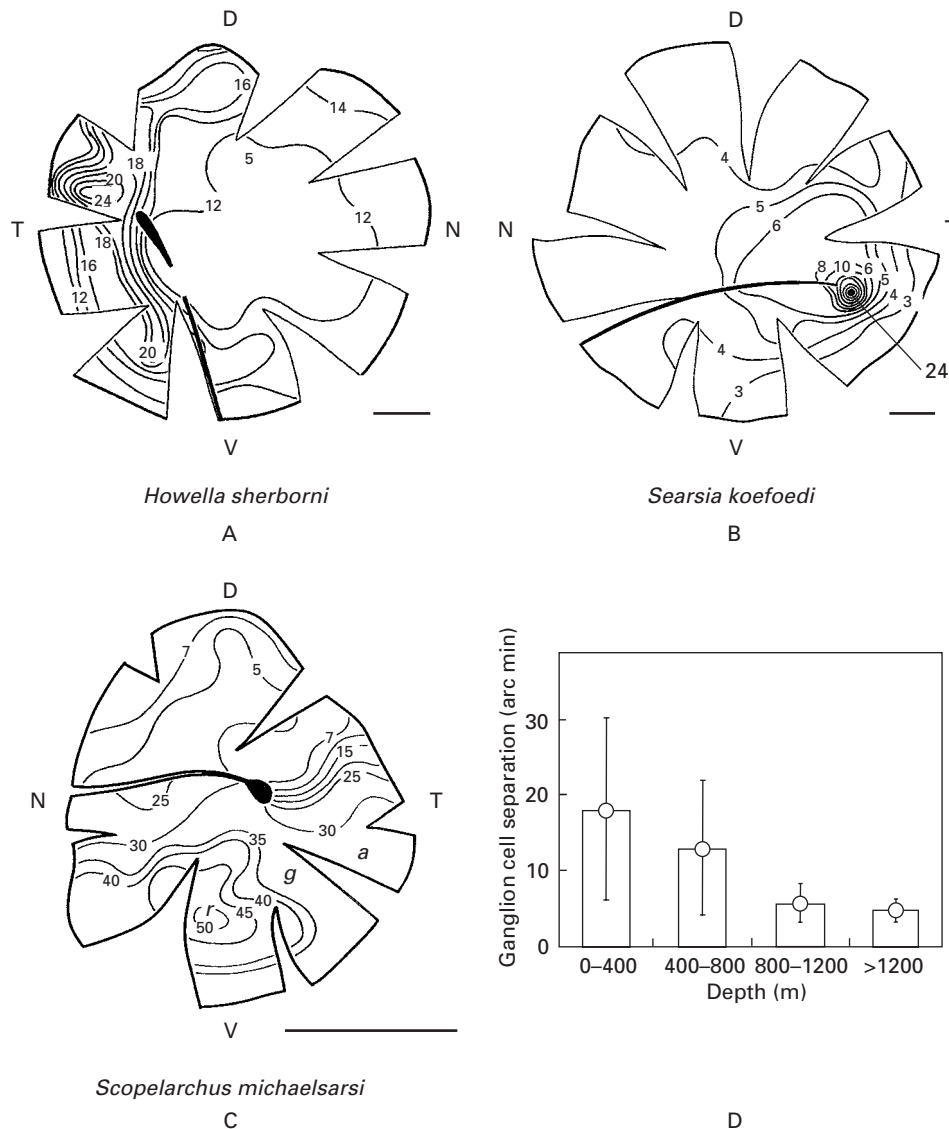


Fig. 11. The transition from extended to point-source visual scenes as reflected in the retinal structure of deep-sea fishes (from Warrant *et al.*, 2003). (A–C) Iso-density contour maps of the distribution of retinal ganglion cells. The retinæ are shown as flat mounts, and densities are given in thousands of cells per mm². T, temporal (with frontal visual field); N, nasal (with posterior visual field); D, dorsal; V, ventral. Scale bar = 2 mm. (A) The deepwater bass *Howella sherborni*, living between 25 and 300 m, has a retina designed to see a bright extended scene with high resolution. Adapted from Collin & Partridge (1996). (B) The platytroctid *Searsia koefoedi*, living between 450 and 1000 m, has a retina optimally designed to see point-source bioluminescence. Adapted from Collin & Partridge (1996). (C) *Scopelarchus michaelsarsi*, living between 250 and 1000 m, has a retina designed to see both extended scenes (using a grouped retina sub-region *g*, and an area of very large ganglion cells, the ‘area gigantea’ *a*), and point sources (using a sharp area centralis *r*). Adapted from Collin *et al.* (1997). (D) The finest separation of ganglion cells found in a survey of 20 species of deep-sea fishes living at different depths, showing mean separation (in arc min) \pm S.D. Deeper-living fishes tend towards sharper retinæ, a reflection of the increasing dominance of bioluminescent point-source illumination with depth.

(eye height ≈ 0.6 mm) adapted for the wide non-directional extended space light, being of quite uniform construction (Fig. 12A), with rather even (but somewhat low) anatomical resolution in all directions of the visual field (Fig. 12B). The eyes of amphipods living at around 200 m – like *Paraprionoe crustulum* (Fig. 12C) – only experience daylight incident from within approximately $\pm 50^\circ$ of vertical (Fig. 1C). In *P. crustulum* (eye height ≈ 4.2 mm) the dorsal part of the eye

has become greatly enlarged, with very large corneal facets adapted to the dim down-welling light ($122 \mu\text{m}$ wide compared to $35 \mu\text{m}$ in *Thamneus* sp.). By contrast, the ventral part is quite small with facets only half as wide. Resolution is not uniform either, becoming significantly better in the dorsal direction, with a clear match to the angular distribution of down-welling light (Fig. 12D). The trend becomes even more extreme in deeper-living species such as

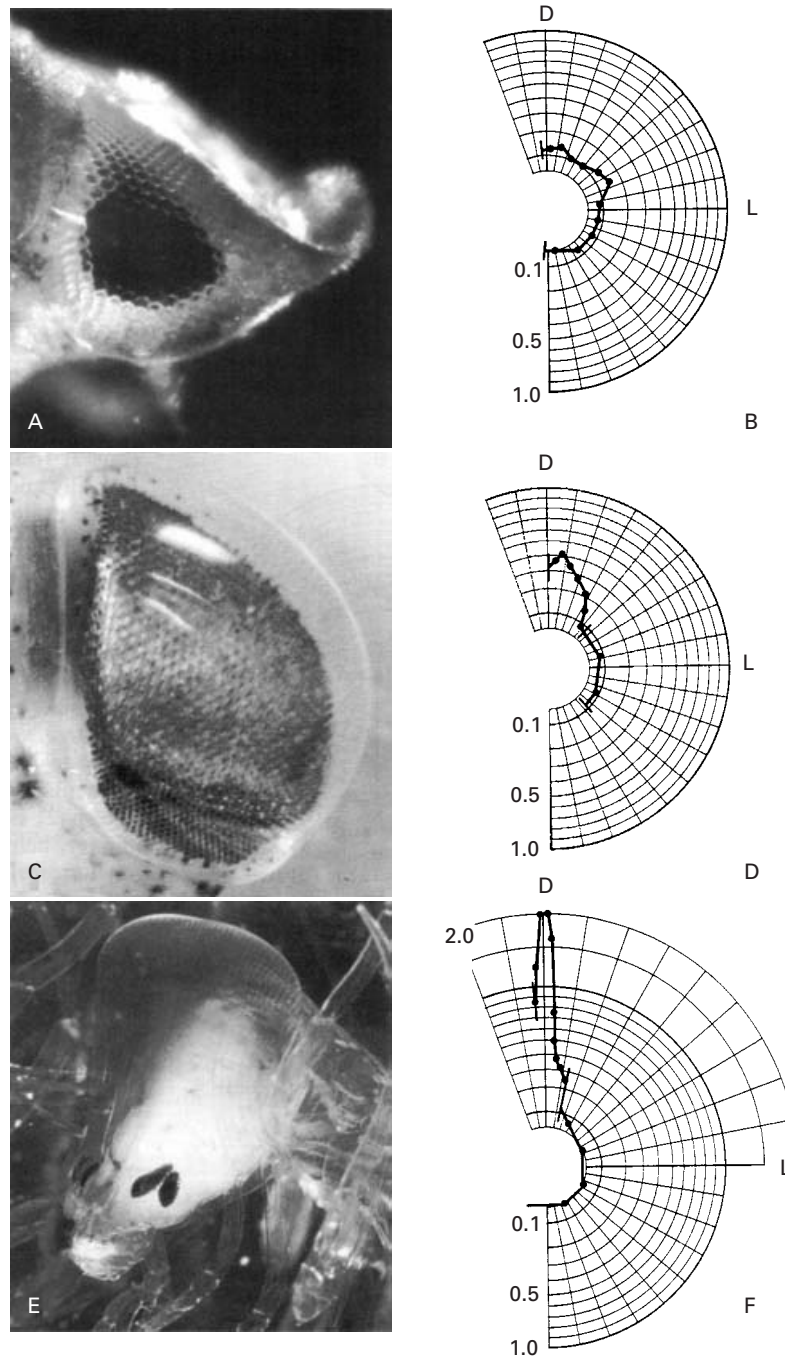


Fig. 12. Eye structure and depth in hyperiid amphipods. Amphipods from different depths are shown at left: (A) *Thamneus* sp., eye height 0.60 mm (surface), (C) *Paraprionoe crustulum*, eye height 4.2 mm (200 m), and (E) *Phronima sedentaria*, eye height 2.4 mm (300–400 m). At right (B, D, F), their respective vertical distributions of anatomical resolution (cycles deg^{-1}) are shown (here calculated as $1/2\Delta\phi$, where $\Delta\phi$ is the interommatidial angle in degrees). Note how resolution in the surface species is low and rather uniform throughout the visual field (B). In deeper species the eye becomes more bilobed, with the dorsal lobe (viewing the down-welling light) dominating. Resolution in the dorsal lobe increases with depth (D, F) and becomes more dorsally directed. D, dorsal; L, lateral. Assembled from Land (1989a).

Phronima sedentaria. In these amphipods, which live between 300 and 400 m, each eye is very large (eye height ≈ 5.5 mm) and entirely divided, with a huge dorsal eye detached from a tiny ventral one (Fig. 12E). The dorsal facets are extremely

large ($146 \mu\text{m}$ wide compared to $80 \mu\text{m}$ in the ventral eyes), and resolution escalates within a narrow (15°) dorsal visual field, outside of which resolution is very poor (Fig. 12F). The receptive fields of the two dorsal eyes also have a high degree

of overlap, a strategy for improving sensitivity that we saw earlier in the dorsal tubular eyes of deep-sea fishes.

What do these depth-related changes in eye design mean? Two of the trends are easy to understand. Firstly, the overall increase in eye size, the increasing extent of overlap in the two dorsal visual fields, and the enlargement of facets, all clearly improve sensitivity. Secondly, the increasingly dorsal bias of the eyes reflects the dominance of dorsal illumination. The third trend is slightly less obvious: with increasing depth, dorsal resolution increases dramatically. In the three species detailed above, interommatidial angle falls from 4.8° in *Thamneus* sp., to 1.1° in *Parapronoe crustulum*, and to an astonishing 0.25° in *Phronima sedentaria*. At the same time, the total dorsal visual field narrows sharply. The explanation can be found by considering what amphipods need to see. Had the eyes been designed to view wide extended scenes, the interommatidial angle should have increased with depth. But if the role of the dorsal eyes is to spot small silhouetted objects floating above, then the opposite would be predicted (Land, 1989a, 2000). Even though the life histories of amphipods are poorly understood, the design of their eyes implies that they use them for spotting small prey animals against the dim down-welling illumination. The same kinds of strategies are also found in the bilobed superposition eyes of many mysids and euphausiid shrimps (krill) (Fig. 13A). Deeper living mesopelagic species have dorsal eyes with more numerous facets and sharper resolution directed into narrower dorsal visual fields (Land, Burton & Meyer-Rochow, 1979; Gaten, Herring & Shelton, 1992a).

It is worth noting that *Phronima sedentaria* has one more remarkable adaptation to the down-welling daylight: a transparent eye that markedly reduces its own silhouette from below. Normally, the screening pigments surrounding the ommatidia of compound eyes are very dark, and in a transparent deep-sea crustacean like *P. sedentaria*, these would cause the eye to cast a very conspicuous silhouette. But in the *P. sedentaria* eye, the pigments are compressed into a tiny bead around the small rhabdoms, creating a minimal silhouette. These rhabdoms are several millimetres away from the facets, and the light they receive is light-guided through long thin extensions of the crystalline cones. The massive fused eye on the top of the head, with its marvellous narrow-field resolution, is almost entirely transparent as a result of this unique light-guiding mechanism (Ball, 1977; Land, 1981b). An alternative solution is to have a retina devoid of screening pigment all together, as in the amphipod *Cystisoma* sp. that we mentioned earlier. In the lower mesopelagic zone where *Cystisoma* sp. lives, bioluminescent point source detection would not be greatly disturbed by the absence of pigment. Even though the extended space light is allowed to leak between the photoreceptors, it is probably too dim to degrade vision.

The directionality of down-welling daylight has also affected the tapeta, which in many deep-sea crustaceans are not equally efficient in all parts of the eye. In decapods, the tapetum is more effective in the part of the superposition eye that looks ventrally, hence increasing sensitivity in this darker part of the visual field (Shelton *et al.*, 1992; Gaten, Shelton & Herring, 1992b; Johnson *et al.*, 2000). The dorsal

eye regions typically have less efficient tapeta, and this may reflect a need for invisibility from above. The narrow angular distribution of down-welling daylight may cause a revealing eye-shine that could be seen by any predator looking downwards. For many species living in deeper water the tapetum becomes less efficient in all parts of the eye, although there are many exceptions (Johnson *et al.*, 2000). In the deepest species there is sometimes very little tapetum at all, an adaptation that may prevent the eye from reflecting the crustacean's own defensive bioluminescent secretions, thus ensuring a covert escape (Shelton *et al.*, 1992). In species from shallower water, with more efficient tapeta, the eye-shine may actually be less revealing, quite likely being weaker than the background space light. Thus, the efficiency of the shrimp's tapetum is the result of a balance between sensitivity requirements and invisibility.

Adaptations for the directionality of down-welling daylight are not confined to the compound eyes of crustaceans. They can also be found in the camera eyes of deep-sea fishes and cephalopods. We have already discussed scopolarchids and hatchetfishes (Fig. 6), with their large dorsal eyes and narrow overlapping visual fields that capture as much of the down-welling daylight as possible, maximising the contrast of silhouetted prey. Some mesopelagic cephalopods, such as *Sandalops* sp. and *Amphitretus* sp., also have dorsally directed tubular eyes that are devoted to the same task (Herring, 2002). In the deep-sea squid *Histioteuthis meleagroteuthis*, one eye is greatly enlarged and somewhat tubular in form, and according to the most popular interpretation, may be pointed upwards – to the benefit of light capture – if the squid swims horizontally (Fig. 13B). The lens is also yellow, suggesting a use in breaking the bioluminescent camouflage of potential prey animals swimming above (see below). However, several observations of *Histioteuthis meleagroteuthis* from the windows of submersibles reveal a quite different behaviour. Instead of being horizontal, they suspend themselves vertically and rotate continuously around their body axis, their big eye apparently scanning the 360° world around them (Bruce Robison, personal communication). However the bright lights of a submersible may severely disorient the animal, so this observation might not represent the squid's natural behaviour.

Spatial resolution in the tubular eyes of fishes – just as in compound eyes – is likewise adapted to the directionality of daylight. Consider the hatchetfish *Argyrops leucops*, which lives in the mid-mesopelagic zone. The ventral part of its main retina has an area centralis of high ganglion cell density (up to $34\,000$ cells mm^{-2}) that samples a narrow dorsal field of view (Fig. 13C; Collin *et al.*, 1997; Wagner *et al.*, 1998). Just as in crustaceans, this high resolution helps fishes localise small silhouetted prey.

(6) Adaptations for breaking mesopelagic camouflage

Ever since the Cambrian explosion, predators have evolved better and more efficient ways of detecting and intercepting their prey. In response, prey animals have evolved mechanisms that more effectively conceal them from detection. This 'arms race' in no small part affects the senses, and

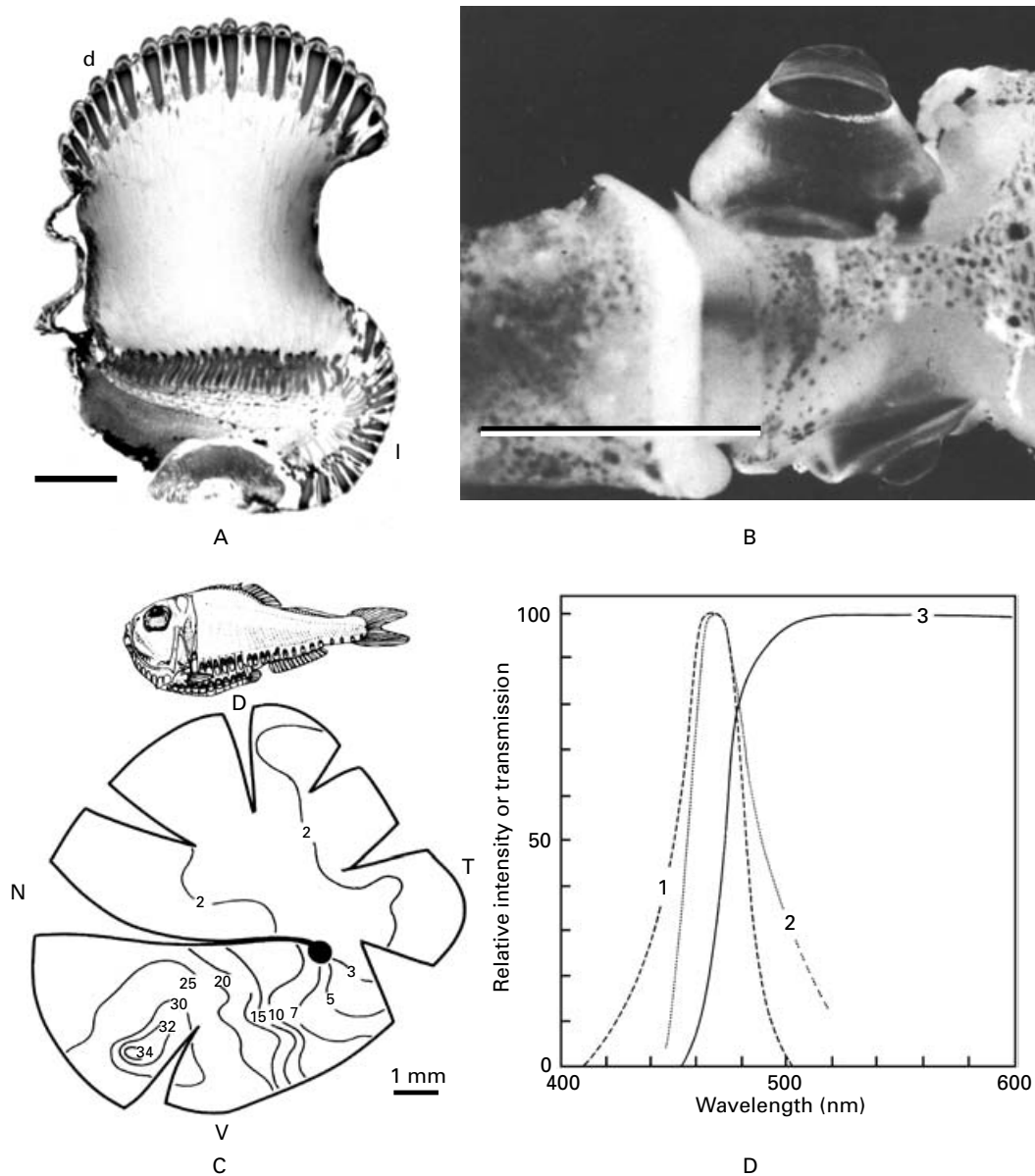


Fig. 13. Visual adaptations for the directionality of light in the deep sea. (A) The divided superposition eye of the euphausiid shrimp *Stylocheiron maximum*. The huge dorsal lobe (d) has a narrow dorsal field of view for viewing the down-welling daylight, while the small lateral lobe (l) has a broader lateral field of view which could be useful for viewing bioluminescent flashes. Photograph courtesy of Dan-Eric Nilsson. Scale bar = 200 μm . (B) Asymmetrically sized eyes in deep-sea squid of the genus *Histioteuthis*. The larger eye has been suspected of viewing the down-welling daylight, although observations of *Histioteuthis* sp. from submersibles suggest otherwise (see text). Scale bar = 10 mm. Photograph courtesy of Michael Land. (C) The dorsally directed tubular eyes of the mesopelagic hatchetfish *Argyropelecus affinis* have well-developed regions of higher resolution in the ventral retina. With its high density of ganglion cells, the ventral retina is ideally constructed to detect small silhouetted objects in the dorsal visual field. All conventions as in Fig. 11. Adapted from Wagner *et al.* (1998). (D) Bioluminescent counter-illumination and the yellow lenses of deep-sea fishes. Counter-illumination produced by the euphausiid shrimp *Euphausia tenera* (curve 2) has a spectrum that is slightly greener than that of down-welling daylight at 500 m (curve 1). The yellow lenses of many deep-sea fishes act as long-pass filters (curve 3) that cut out most of the down-welling blue light and accentuate the difference between the counter-illumination and the remaining daylight. Adapted from Munk (1980).

especially the visual system. If a prey animal evolves a mechanism to make itself less visible, then its predator will evolve a visual mechanism to overcome it. Few habitats on earth reveal this better than the mesopelagic zone.

As we saw earlier, many mesopelagic animals hide themselves from below using bioluminescent counter-illumination. Unfortunately, the colour of the counter-illumination produced by the photophores does not exactly

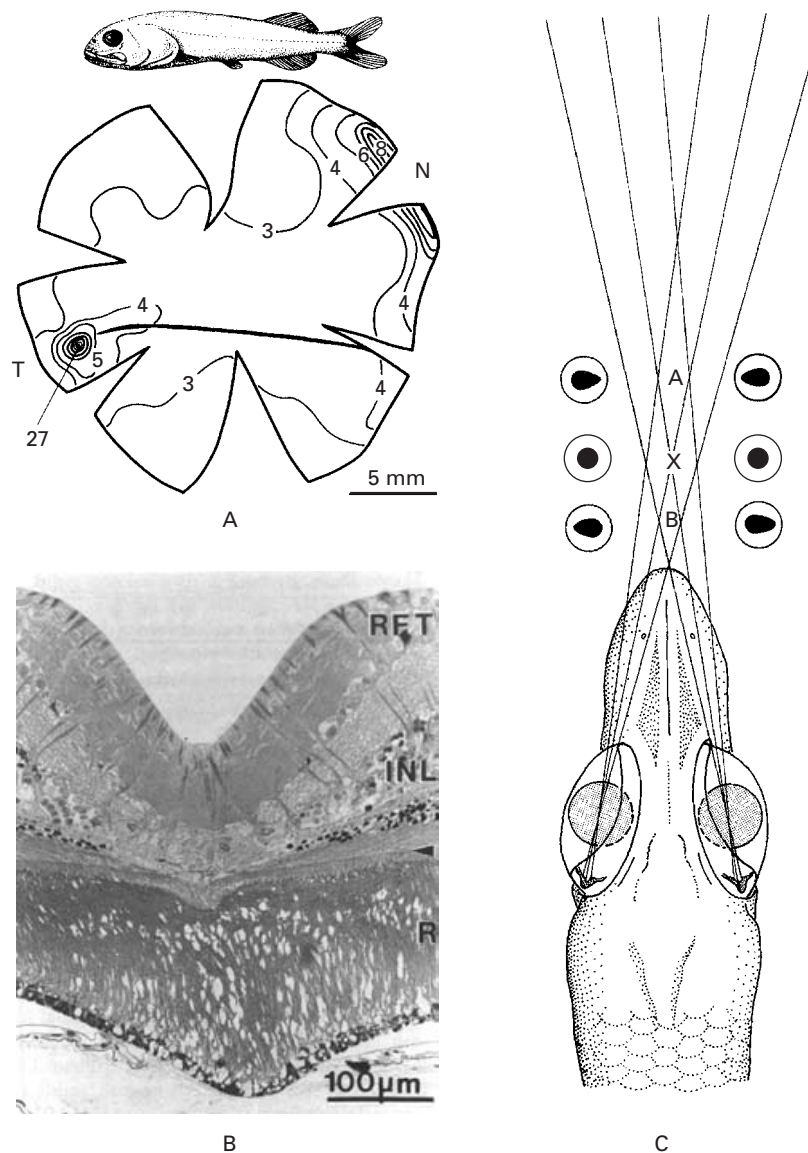


Fig. 14. Visual adaptations in bathypelagic fishes (from Warrant *et al.*, 2003). (A) *Rouleina attrita* has a retinal design that is common in bathypelagic fishes, with deep convexitivate temporal foveae containing densely packed ganglion cells. This design is ideal for localising bioluminescent point sources in the frontal visual field. All conventions as in Fig. 11. (B) A transverse light microscope section through the deep convexitivate fovea of the alepocephalid *Conocara macroptera*, a fish living in the bathypelagic zone down to 2.2 km. *RFT*, radial fibre layer; *INL*, inner nuclear layer; *R*, rod photoreceptors. (C) A possible role for deep convexitivate foveae in determining the range of bioluminescent point sources. Range may be calculated using the extent and direction of image skewing within the steep sides of the foveal pit in each eye. See text for details. All panels adapted from Wagner *et al.* (1998); (C) adapted from Locket (1985).

match that of the surrounding daylight, having a spectrum slightly broader on the green side of the emission peak. Some fishes, like the scopolarchids, may see this subtle difference using colour vision based on two or more visual pigments (see above). But even without colour vision, the dorsal eyes of many deep-sea fishes can pick out this difference by having lenses that contain yellow pigment. Such lenses selectively remove the blue part of the spectrum, paradoxically cutting out most of the light that could have reached the retina (Fig. 14D; Munk, 1980; Douglas &

Thorpe, 1992). By performing this long-pass filtering, yellow lenses remove most of the background light, thereby enhancing the slightly greener counter-illumination (Muntz, 1976; Somiya, 1976). The unsuspecting prey, instead of being camouflaged, now shines like a torch.

A similar strategy has also been proposed for mesopelagic cephalopods, but one that is instead based on polarisation sensitivity (Hanlon & Shashar, 2003). The rhabdoms of many cephalopods are built from orthogonal stacks of microvilli, and are thereby intrinsically sensitive to polarised

light. Although this remains to be tested, Hanlon and Shashar (2003) postulate that the bioluminescent counter-illumination of many organisms may become polarised after reflection from the iridophores that line the photophores. If this is true, counter-illumination will be highly visible to cephalopods (and crustaceans) that are able to see polarised light. Against a background of unpolarised down-welling daylight, the telltale silhouettes of counter-illuminating animals will dramatically reappear for any animal able to see polarised light.

The ability to see polarised light is useful for breaking other kinds of camouflage as well. Due to the arrangement and order of their internal tissues, many transparent animals change the polarisation characteristics of the light that passes through them, either by depolarising the light completely, or by rotating its polarisation plane (Johnsen, 2001). In other words, to an eye sensitive to polarised light, transparent animals are no longer transparent. The epipelagic squid *Loligo pealei* has been shown to distinguish transparent objects on this basis (Shashar, Hanlon & Petz, 1998), and to use this ability for detecting transparent prey. Presumably many crustaceans have similar abilities. Other cephalopods, like the shallow water cuttlefish *Sepia officinalis*, might use their polarisation vision to break the silvering camouflage used by many fishes (such as herrings) to hide themselves in the down-welling light. This type of camouflage generally works very well, because most predators are unable to detect the fatal flaw in the strategy: the silvery sides of fishes reflect partially linearly polarised light (Land, 1984*b*; Shashar *et al.*, 2000). Cuttlefishes see this reflected polarised light and use it to discriminate fishes during hunting (Shashar *et al.*, 2000). It is still unclear whether the use of polarisation vision for breaking transparency and silvering works at depth. Certainly in the bright epipelagic depths, where polarised light abounds, transparency breaking is a useful strategy. This is probably even true of the upper 100–200 m of the mesopelagic zone. But in the middle and lower mesopelagic zone, where the degree of polarisation is low (probably only between 13 and 38%: Waterman, 1981), it is still uncertain what role, if any, polarisation vision might play in transparency breaking. On the other hand, the use of polarisation vision to break silvering camouflage – which does not require a polarised space light – is useful at all mesopelagic depths.

The ability to see ultraviolet (UV) light also provides an enormous potential for breaking camouflage, particularly transparency (Johnsen & Widder, 2001; Johnsen, 2001), but again its usefulness is probably greatest in the brighter upper depths of the ocean. Biologically significant levels of UV light probably only penetrate the upper 200–300 m of the ocean (Frank & Widder, 1996; Losey *et al.*, 1999). Many marine animals – especially fishes and crustaceans active in the UV-rich shallows – are able to see and use UV light (reviewed by Losey *et al.*, 1999). Surface-living transparent animals are often quite opaque in UV light (reviewed in Johnsen & Widder, 2001), and thus visible to predators capable of seeing in this spectral range. The juvenile rainbow trout *Oncorhynchus mykiss* uses its well-developed UV sensitivity successfully to hunt the branchiopod *Daphnia pulex*, which loses its transparency in full-spectrum

illumination that includes UV light. In illumination lacking UV, the sighting distance for *D. pulex* is shorter, and the trout is much less successful in capturing prey (Browman, Novales-Flamarique & Hawryshyn, 1994). In the deep ocean, at depths below the penetration of biologically useful UV light, it is unlikely that transparency camouflage can be broken using UV vision (unless there are animals that can produce their own UV light). In addition, UV sensitivity is rare in deep-sea animals, although interestingly it has been found in four species of photophore-bearing mesopelagic oplophorid shrimps (Frank & Case, 1988; Cronin & Frank, 1996), suggesting a possible role in intraspecific communication.

VII. ADAPTATIONS FOR VISION IN THE BATHYPELAGIC ZONE

‘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’ (Marshall, 1979). This description of life and nutrition at depths below 1000 m paints the bathypelagic zone as a dark world with little food, where most animals have been forced to adopt extremely low respiration rates to survive. Their muscles are watery and weak, their skeletons flimsy and their internal organs diminished. Compared to their relatives from brighter shallower waters, bathypelagic creatures (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, de Ruyter van Steveninck & Anderson, 1998). But as we shall see, far from their reputation as being regressed, the eyes of many bathypelagic animals are surprisingly sophisticated.

(1) The visual world of the bathypelagic zone: a realm of fitful sparks

Marshall’s ‘fitful sparks’ of bioluminescence – rare and often dim – are the only things bathypelagic eyes see. But failing to see a bioluminescent flash could mean missing a rare meal, or losing a seldom-encountered mate. To localise a flash accurately requires reliable detection (i.e. good sensitivity to a point source), precise discrimination of the direction of the flash (i.e. good spatial resolution) and some mechanism for determining how far away the flash was (i.e. good depth discrimination). The first two are functions of the optical design of an eye, and are straightforward adaptations. But to determine the range of a flash against a dark background is far from trivial (Walls, 1942). Terrestrial animals like ourselves rely on many cues to judge the distance of objects, including disparity calculations (which require our eyes to be a reasonable distance apart), parallax effects, perspective cues and learned features of object size. For bathypelagic animals all but the first of these are absent. Even the remaining cue – disparity – is severely hampered by the generally small heads and limited eye separations

typical of bathypelagic animals. Flash brightness cannot be used as a cue, because it is impossible to distinguish a dim flash that is close from a bright flash that is further away. It is still far from clear how bathypelagic animals cope with this demanding task, but in fishes at least, specialised retinal adaptations could provide the solution, as we shall see below.

(2) The eyes of bathypelagic fishes

With a few notable exceptions, the eyes of bathypelagic fishes tend to be smaller (relative to body size) than those of their mesopelagic relatives. Tubular eyes, so common in the lower mesopelagic zone, are now almost completely absent. A few species, like some whalefishes, have eyes that are clearly regressed, with defective or absent lenses and degenerate retinæ (Munk, 1966; Marshall, 1971). Others, like the alepocephalids, have large and highly developed eyes (Marshall, 1971), and apparently rely much more on vision than on other senses (such as olfaction: Collin, Lloyd & Wagner, 2000). This sizeable variation in eye development, and thus in the relative importance of vision, certainly reflects variation in the natural histories of bathypelagic fishes. Sadly, the details of these natural histories remain rather sketchy.

Despite their generally small size, the eyes of most bathypelagic and abyssal fishes are perfectly functional. They are certainly of sufficient sensitivity and resolution to detect point-source flashes of bioluminescence, especially over ecologically meaningful distances. We have already discussed the two features required in a bathypelagic eye to maximise sensitivity to a point source (equations 3–5): a wide pupil and long absorbent photoreceptors with little intrinsic dark noise. Bathypelagic fishes do tend to have large pupils relative to eye size compared to their mesopelagic cousins, with pupil diameters of 12 mm or more not being uncommon (Wagner *et al.*, 1998). Nothing is so far known about levels of dark noise, but the low water temperatures of the deep probably keep it low. Nevertheless, even low levels can severely limit sensitivity (see Section V). We also saw in Section V that an average bathypelagic fish with a pupil diameter of 7.3 mm and a dark noise of 0.0001 s^{-1} could see a blue bioluminescent flash containing 10^{10} photons up to almost 100 m away (Fig. 3A). What does this range mean for a bathypelagic fish?

For a start, a flash that is 100 m distant might as well be in another ocean. Most bathypelagic fishes simply lack the energetic capacity to reach flashes this far away. Typical swimming speeds are in the order of one body length per second (Marshall, 1979), so for a fish that is 10 cm long, a flash 100 m away would take approximately 17 min to intercept. By then the producer of the flash could have moved far away, and the fish, having expended much precious energy, would have little chance of finding its potential mate or prey. Even though bathypelagic fishes can see distant flashes, they probably only react to those occurring at much closer range.

Large and overly sensitive eyes might actually be disadvantageous for bathypelagic fishes. Smaller and less sensitive eyes, in addition to being energetically less expensive, reduce

the range of bioluminescent visibility, thereby cutting out many of the impossibly distant flashes that might otherwise have been tempting to pursue. Instead, visible flashes would be more likely to occur within a realistic range of interception. A fish with a pupil just 1 mm wide can only see the average flashes mentioned above within a range of 47 m (Fig. 3A), compared to 100 m with a 7.3 mm pupil.

Once eye size has limited the range of detection, other mechanisms – such as those based on the disparity of images formed in the two eyes – can more accurately determine the range of a flash. Disparity calculations rely on the very slight difference (or disparity) in the position of images formed on the left and right retinæ due to the finite separation of the eyes. The disparity is greater for a flash that is closer than for a flash that is further away, and therein lies the brain's method for calculating the distance of the flash. Essential to the calculation is an accurate determination of the disparity, and this requires binocular vision, reasonable eye separation and good spatial resolution. Greater separation and sharper resolution allow a more accurate determination of disparity, and a more reliable estimation of distance.

Some bathypelagic fishes are large and have the potential for wide eye separation. This however is not the case for the very large number of species that are shorter than 20 cm. Spatial resolution, on the other hand, is surprisingly good, with foveal ganglion cells typically separated by just 5 minutes of arc (see Fig. 11D). An excellent example is *Rouleina attrita* (Fig. 14A), a fish living near sea floors between 1.4 and 2.1 km below the sea surface (Wagner *et al.*, 1998). This fish has sharp frontally directed foveae possessing up to $27\,000$ ganglion cells mm^{-2} . With rostral aphakic apertures, and deep convexiculate temporal foveae, the eyes of *R. attrita* (and many other similar species) are clearly designed for accurately localising bioluminescent point sources in the frontal visual field.

Deep convexiculate foveae (Fig. 14B) may also play a role in determining the range of bioluminescent flashes that occur within the visual fields of both eyes (Lockett, 1985, 1992). The steep curvature, and slightly higher refractive index of the radial fibre layer that lines the foveal pit, have the potential to alter, and even distort, the focus of incoming light rays. Assuming that the axes of the two eyes are fixed and converging, the lines of sight of the foveal centres will cross at a particular point *X* in front of the fish. A point source located at *X* will be imaged symmetrically by the steep-sided foveal pit in each eye (Fig. 14C), resulting in perfectly round blur-circle images that are slightly magnified (the pit acts as a weak negative lens). If the point source is located closer to the fish than *X* (point *B* in Fig. 14C), the steep lateral sides of the pits distort the images, skewing them into comet-like shapes, with the 'tail' of each comet pointing laterally across the retina. This image skewing is more pronounced for point sources closer to the fish. The opposite is true of a point source located further away than *X* (point *A* in Fig. 14C): the steep medial sides of the foveal pits skew the images such that their 'tails' point medially, the extent of skewing increasing for point sources further away. If the fish can measure the extent and direction of image skew it has a way of calculating the range of point sources.

These adaptations – rostral aphakic apertures, deep convexiculate foveae, sharp spatial acuity and paradoxically small eyes – all allow bathypelagic fishes to localise points of bioluminescence accurately in the immense darkness. Even though the nutritional poverty of the bathypelagic zone, and the unreliability of distance estimations, limit this localisation to distances of less than a few tens of metres, there is no question that the eyes of bathypelagic fishes are well adapted for life in a world of point sources.

(3) The eyes of bathypelagic crustaceans and cephalopods

Compared to their mesopelagic relatives, many bathypelagic crustaceans have extreme adaptations for capturing light, although some have also clearly succumbed to the darkness. Many species have eyes that are severely reduced, and these animals presumably rely on other senses. The bathypelagic hyperiid amphipod *Scypholanceola* sp. is a good example, with reduced eye size, optics and ommatidial numbers. Only a naked retina remains, behind which exist two reflectors (Land & Nilsson, 2002, p. 110). But for those with well-developed compound eyes, the overriding goal is to capture light. Because compound eyes resolve poorly for their size compared to camera eyes (Kirschfeld, 1976), they are incapable of having enough sensitivity to detect reliably a bioluminescent point source while at the same time maintaining enough spatial resolution to localise it accurately (as bathypelagic fishes have mastered). In this impossible equation, bathypelagic crustaceans have invested in sensitivity. Their eyes imply they are unable to distinguish the exact locations of bioluminescent sources. Rather, they should only be able to distinguish whether or not a source is present (Land, 2000). Nevertheless, active swimmers like the giant bathypelagic ostracod *Gigantocypris mülleri* – with its impressive mirror eyes – might gain an impression of the location of bioluminescent point sources by moving relative to them.

As in fishes, the eyes of bathypelagic crustaceans are often quite reduced. The bathypelagic euphausiid *Thysanopoda minyops*, which lives at immense depths between 3500 and 5000 m, has minute eyes with very few ommatidia. Another bathypelagic euphausiid, *Bentheuphausia amblyops*, also has very small eyes, with a very disorganised facet arrangement (Hiller-Adams & Case, 1984, 1988). Many bathypelagic mysids have small or degenerate eyes, some lacking optical elements and possessing hypertrophied rhabdoms (Herring, 2002).

Not all compound eyes in bathypelagic crustaceans are small or degenerate. Some have large eyes with huge corneal facets and massive rhabdoms, adaptations that maximise the sensitivity of the eye to bioluminescent point sources (equations 3–5). The apposition eyes of the anomuran half-crab *Paralomis multispina*, found at depths of 1200 m, have facet diameters of 60 μm and rhabdoms 25 μm wide and 210 μm long (Eguchi, Dezawa & Meyer-Rochow, 1997; Meyer-Rochow & Nilsson, 1998). The world's largest isopod, the bathypelagic *Bathynomus giganteus*, has corneal facets up to 140 μm wide (Chamberlain, Meyer-Rochow & Dossert, 1986), in an eye that

nevertheless contains 3500 ommatidia and presumably passable resolution!

The record for the most sensitive crustacean eye probably goes to the large reflector eyes of the ostracod *Gigantocypris mülleri* (Land, 1981*a*). These eyes have reflectors that look like car head-lamps, measuring 3 mm across and having large overlapping visual fields. These, and enormous photoreceptors (25 $\mu\text{m} \times 700 \mu\text{m}$), give this animal a truly impressive sensitivity. But reflector eyes resolve poorly, and again the same principle applies as for compound eyes: the presence or absence of bioluminescence, rather than its location, seems to be the overriding priority in the design of the bathypelagic crustacean eye.

The eyes of bathypelagic cephalopods are frequently reduced in size like those of fishes but apparently fully functional (Herring, 2002), like those of the octopod *Cirroteuthis* sp. One species of bathypelagic squid – *Bathyteuthis* sp. – has a well-developed fovea (Chun, 1914; Hanlon & Messenger, 1998; Herring, 2002), suggesting a use in detecting point-source bioluminescence.

VIII. ADAPTATIONS FOR VISION IN THE BENTHIC HABITAT

The open sea floor possesses two very important properties of great relevance to vision. Firstly, throughout much of the ocean, the sea floor is a vast plain that constrains its non-swimming occupants to exist within a flat two-dimensional world. By contrast, the pelagic environments above are entirely three-dimensional. Secondly, the sea floor is the repository of a continuous downward rain of organic matter that endows it with a rich nutrient level and fuels an active food web (Marshall, 1979). Compared to their cousins in the pelagic environments, animals that cruise near the bottom have taken advantage of this better nutrition, and tend to be stronger swimmers. Some species also have surprisingly well-developed eyes, even at depths beyond the penetration of daylight.

(1) The visual world of the benthic habitat: seeing in two dimensions

A sea floor lit by daylight is clearly visible to any animal with sufficiently sensitive eyes. The interface between the muddy bottom and the water above creates a single dominant visual feature – the horizon – a feature that also defines where other objects of visual interest are likely to be located. Animals taking advantage of the nutritional benefits of the sea floor may cruise slowly above it, scanning the horizon ahead for smaller animals upon which to prey. This horizontally constrained world of hunters and the hunted is not unlike the open plains of Africa. As we will see, some of the same kinds of visual adaptations that evolved for the open-plains environment also evolved in the benthic habitat.

A sea floor located beyond the penetration of daylight also has the potential to provide a dominant horizon of visually interesting features, although at this stage, this possibility is purely speculative. Like the blinking lights of

a sparsely populated landscape seen from an aeroplane at night, the wide open sea bottom is home to an enormous variety of bioluminescent invertebrates. Shrimps, sepiolid squids, brittle stars, sea stars, sea lilies, sea cucumbers, sea spiders, polychaetes, corals, sea pens and sea pansies are but a few of the common benthic and benthopelagic invertebrates that are bioluminescent (Marshall, 1979; Herring, 2002). Many of these are thought to light up when an active swimmer brushes over them. The beautiful deep-sea bamboo coral is a marvellous example. This coral secretes a slimy bioluminescent coating that glows bright blue when disturbed. If sufficient densities of such animals exist – and in some places they do – a bottom-cruising fish may leave behind an undesirable glowing record of its journey, no doubt highly visible to any predator lurking above. But the risk might be worth it. Some fishes might even use this light as a way of illuminating their own prey.

(2) The eyes of benthic and benthopelagic fishes

Like the eyes of fishes inhabiting different pelagic depths, the eyes of fishes inhabiting sea floors at different distances below the sea surface show characteristic changes in form with depth. Marshall (1954, 1971) vividly describes these changes in the bottom-dwelling swimbladder-lacking liparids (sea-snail fishes), and in the benthopelagic macrourids (rat-tails) and brotulids. Species living in and over sea floors that are dimly lit by down-welling daylight have comparatively large eyes relative to head size, and retinæ packed with rods. The deeper the sea floor, the larger the eyes. As already discussed, larger eyes can better distinguish a dim extended habitat. In species living on sea floors below 1000 m, the trend tends to reverse. With a few notable exceptions (see below), eyes progressively decrease in relative size, and at abyssal depths can become very small indeed, some little more than a small black point buried in the skin. Despite their tiny size, many of these eyes are fully functional. But others are clearly degenerate, like those of hagfishes, or even nearly absent, like the two curious large plate-like structures covering the top of the flattened head of the bottom-dweller *Ipnoops murrayi* (Munk, 1959; Locket, 1977). These eyes have no discernible cornea, iris or lens and are thereby incapable of providing a focused image. Instead, a thin transparent membrane of bone overlies a flat sheet of rods and a poorly differentiated layer of second and third order neurons. Ganglion cells appear to be absent. These eyes, like those of the bathypelagic crustaceans we discussed earlier, would do little more than simply detect the presence or absence of bioluminescence, but probably rather well. Presumably these and other visually impaired fishes rely heavily on other senses to find food within the dark oozes of the bottom. In the words of Walls (1942, p. 398): 'Life on the bottom is largely life in one plane, and the finding of food by touch and chemoreception is vastly easier. Go far enough along the bottom (if you're a fish), and you're bound to bump into something good to eat'.

Such eyeless hit-and-miss detection of food is by no means the rule. Nor is the trend for decreased eye size with depth. Many strongly swimming rat-tails and alepocephalids have large, well-developed eyes with frontal visual fields

(Marshall, 1954, 1971; Wagner *et al.*, 1998), a feature that is reflected in their typically large optic tecta (Wagner, 2001a). These fishes cruise above sea floors as far down as 5 km, and their eyes suggest they are active visual predators. What are they looking at? Unfortunately so little is known about the lives of these fishes that one can only speculate on the basis of their eye designs. Many alepocephalids – like *Rouleina attrita* (Fig. 14A) and *Bathytroctes microlepis* (Fig. 15A) – clearly have eyes designed to localise bioluminescent point sources accurately in the frontal visual field, with deep convexiculate temporal foveae of high spatial resolving power and pupils that incorporate a frontal aphakic gap (Locket, 1992; Wagner *et al.*, 1998). Curiously, the sizes of their eyes and pupils tend to be much larger than required to detect bioluminescent point sources at meaningful distances (as discussed above for bathypelagic fishes). They instead seem better sized for the detection of an extended scene. But how would this be possible without daylight illumination? One intriguing possibility – and admittedly one that is purely speculative – is that the fishes themselves can either produce or induce extended bioluminescent illumination of the sea bottom and any potential prey upon it. Many rat-tails harbour colonies of bioluminescent bacteria within an open gland along the belly (Marshall, 1971), and if close enough, could easily illuminate the sea floor. Even fishes lacking this gland might mechanically induce bioluminescence in bottom-dwelling invertebrates to achieve the same effect. Many of these invertebrates are highly bioluminescent, and some of them, like bamboo corals, can be large and fan-like. If sufficiently disturbed, bamboo corals might create light shows of considerable brightness and spatial extent. Alas, we still do not know if this type of bioluminescent sea-floor illumination really occurs, but the large eyes of many benthopelagic fishes could easily take advantage of it.

The visual horizon provided by the flat ocean floor – and the predictable concentration of animal life that its presence has ensured – has also had a striking effect on the design of deep-sea eyes. In the benthic habitat, the likelihood of potential predators and prey is greatest at or near the horizon of the sea floor, and animals that depend on seeing them accurately would be well served by having heightened visual performance directed along this same horizon. In African plains animals, like the large predatory cats and their antelope prey, this heightened performance is due to the presence of a horizontal 'visual streak', an elongated strip of densely packed ganglion cells whose horizontal orientation is exactly aligned with the horizon and all animals located there. Similar retinal adaptations are also found in marine animals. Visual streaks are common in shallow-water fishes living on bright sandy bottoms (Collin & Pettigrew, 1988), but until recently were unknown in deep-sea fishes. Several species of bottom-cruising deep-sea sharks are now known to possess visual streaks (Bozzano & Collin, 2000), including species inhabiting sea floors illuminated by daylight (Fig. 15B), and others that inhabit sea floors beyond the penetration of daylight (Fig. 15C). The peak ganglion cell density of these streaks is, however, rather low – typically approximately 2300 cells mm⁻² – 12 times lower than found in the point-source-detecting deep foveae of the

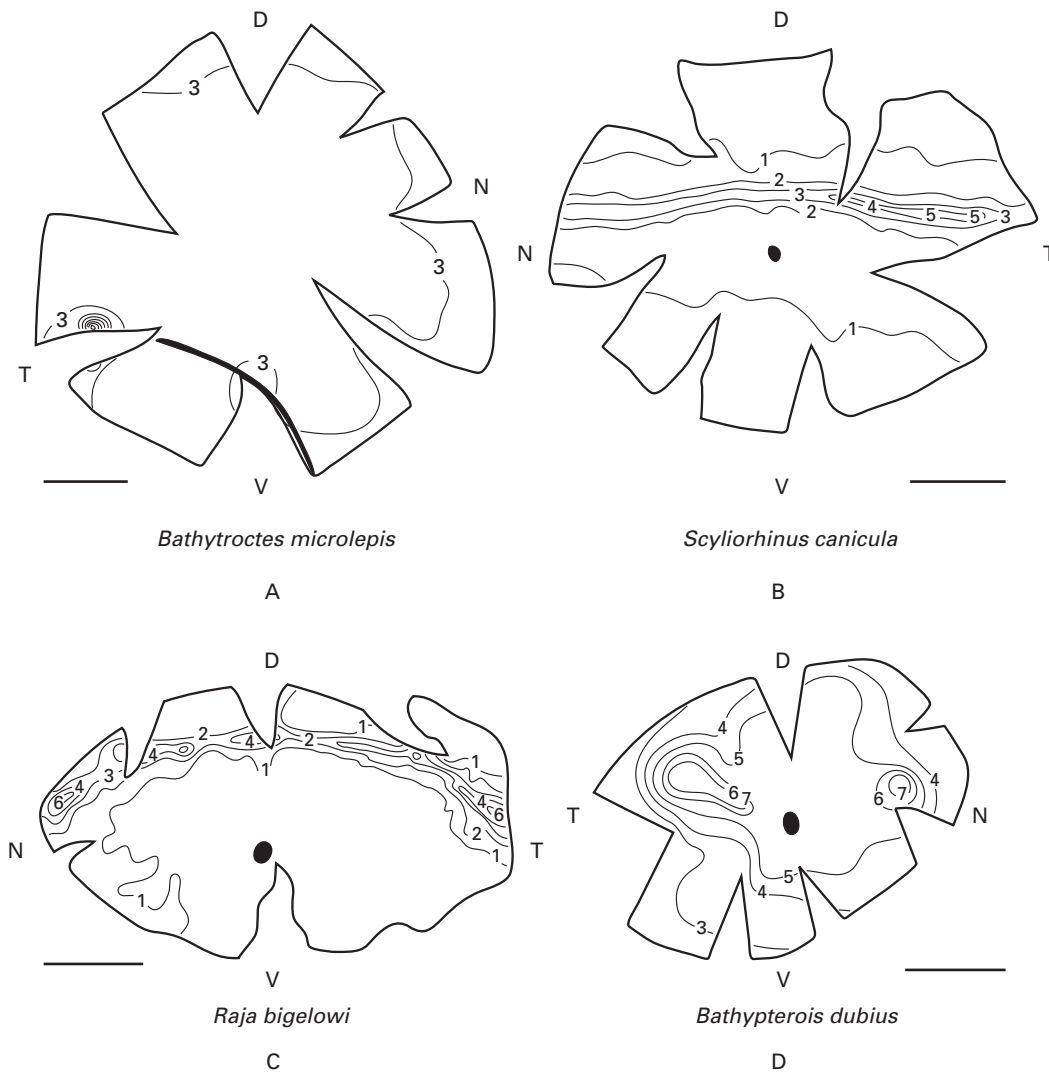


Fig. 15. Visual adaptations in benthic and benthopelagic fishes (from Warrant *et al.*, 2003). (A) The alepocephalid *Bathytroctes microlepis*, which cruises sea floors lying 1.1–2.7 km below the surface, clearly has eyes adapted for seeing bioluminescent point sources in the frontal visual field. Re-drawn from Collin & Partridge (1996). (B) The retina of *Scyliorhinus canicula*, a benthic shark that inhabits sea floors down to 400 m, has a horizontal visual streak aligned with the dimly illuminated visual horizon. Re-drawn from Bozzano & Collin (2000). (C) *Raja bigelowi*, a benthic shark that inhabits sea floors down to 2.2 km, also has a horizontal visual streak, possibly for viewing a sea bottom illuminated by bioluminescent animals. Re-drawn from Bozzano & Collin (2000). (D) The tripod fish *Bathypterois dubius*, which sits on sea floors down to 2 km, has a retina with two areas of high sensitivity, one pointing frontally, the other pointing backwards. This may be a useful design for the tripod fish's sit-and-wait predatory lifestyle. Re-drawn from Collin & Partridge (1996). Scale bars = 5 mm (A–C), 1 mm (D). All conventions as in Fig. 11.

bathypelagic fishes we discussed earlier (Fig. 14). This suggests a role in detecting dim extended features with high sensitivity. The visual streaks shown in Fig. 15B and C are placed somewhat dorsally in the two retinae, implying a more ventral field of view than might be expected for a shark cruising exactly at the bottom. If, as is more likely, the shark swims some metres above the bottom, the horizon and all animals located there will appear in the ventral visual field and would be better seen by a dorsally placed visual streak. In species like *Raja bigelowi* (Fig. 15C), which can cruise sea floors that lie 2 km below the surface, the visual streak could

be used to scan the unseen horizon ahead, the most likely direction where prey might be encountered. Benthic fishes, unwittingly illuminating themselves by setting off the bioluminescent alarm systems of sea-floor invertebrates, would then be accurately seen and intercepted.

A fish that spends all its time in the oozes of the sea floor might also have use of a horizontal visual streak, but this is not what one finds in its retina. The tripod fish *Bathypterois dubius* – which orients against the oncoming current and props itself up on the bottom with the help of its stiffened pelvic and caudal fins – lacks a visual streak (Fig. 15D).

Instead, it has a retina with an even and rather low ganglion cell density that increases slightly within two 'areae retinae', one pointing frontally and slightly ventrally, the other pointing backwards (Wagner *et al.*, 1998). Unlike deep-sea sharks, the tripod fish is a sit-and-wait predator that feeds on small bioluminescent copepods that wash by in the current. The temporal (frontally directed) areae retinae might be used to detect a copepod that suddenly appears in the frontal-ventral visual field. This task is very different to scanning an extended horizon while cruising above the bottom. Waiting for prey is better suited to an enhanced retinal region that is directed towards the part of the visual field where prey is expected to arrive.

(3) The eyes of benthic and benthopelagic crustaceans and cephalopods

The eyes of benthic crustaceans share many of the qualities that are characteristic of benthic fishes. The better nutrition found on the sea floor favours more agile crustaceans with larger eyes compared to those found in the relatively impoverished pelagic depths above. The possibly greater abundance of bioluminescent signals at or near the bottom would also favour better eyes (Herring, 2002). The larger eyes of benthic crustaceans also tend to have longer and wider rhabdoms that improve sensitivity, and being large, the eyes can also have higher resolution. Interestingly, eyes are generally larger in benthic crustaceans living on sea floors at greater depths (Hiller-Adams & Case, 1985), a trend we saw earlier for many groups of benthic fishes.

One of the most sensitive compound eyes of all is found in a benthic crustacean, and strangely, it is an apposition eye. The deep-sea isopod *Cirolana borealis*, which can be found on sea floors down to 1200 m, has apposition eyes possessing just 60 ommatidia. These ommatidia are gigantic compared to those of relatives living in much shallower water (Fig. 16B; Nilsson & Nilsson, 1981). Very large corneal lenses (150 μm wide) of short focal length (100 μm), and huge rhabdoms (90 $\mu\text{m} \times 90 \mu\text{m}$) sitting in cups of reflective pigment, endow *C. borealis* with a sensitivity of 5091 $\mu\text{m}^2 \text{sr}$. As in *Oplophorus spinosus* this very high sensitivity comes only at the cost of resolution: in *C. borealis*, the ommatidia have visual fields of approximately 45° , and are separated from one another by an angle of between 10° and 20° . But for the scavenging lifestyle that *C. borealis* leads, sensitivity is probably of greater importance. Indeed, its close relative *Aega* sp. has 300 ommatidia and is an active hunter, a lifestyle that probably demands better visual acuity (Nilsson & Nilsson, 1981).

There are of course many benthic invertebrates that have reduced eyes. Indeed, some have lost their eyes completely, like the squat lobster *Munidopsis crassa* (Herring, 2002). Others have degenerate eyes, like the finned octopod *Cirrothauma murrayi* (Fig. 16C; Chun, 1914; Aldred, Nixon & Young, 1978, 1983), which can be found on and above sea floors below 3000 m (Hanlon & Messenger, 1998). This octopod lacks photophores and has a markedly reduced visual system. Its eyes (which are 14 mm in diameter) lack lenses and the optic lobes are small and simply organised. Despite their small size, the eyes are probably sufficient to detect the bioluminescence produced by other animals.

The bresiliid shrimps are another good example of an invertebrate with reduced benthic eyes. Lacking optical elements, the eyes of these shrimps mostly consist of enlarged flattened sheets of naked rhabdoms. In one case – the shrimp *Rimicaris exoculata*, which inhabits hydrothermal vents (Fig. 16A) – this sheet has become embedded in reflective material and incorporated into the carapace (van Dover *et al.*, 1989; Gaten *et al.*, 1998; Chamberlain, 2000). A similar design is also found in the adult vent crab *Bythograea thermydron* (Jinks *et al.*, 2002). The eyes of *Rimicaris exoculata* are reminiscent of those of the benthic fish *Ipnops murrayi* that we discussed earlier. Just as in *Ipnops murrayi*, the fused eyes of the vent shrimp act as a large flat photodetector, incapable of resolving focused images. The naked-retina eyes of *Rimicaris exoculata* and *Bythograea thermydron* can do little more than judge the intensity of the light falling on them.

There is still much speculation about what the eyes of *Rimicaris exoculata* and *Bythograea thermydron* might be looking at. Hydrothermal vents are chimney-like structures in the sea floor that spew extremely hot water (approximately 350°C) from the interior of the earth (see Herring, 2002, chapter 3). The hot water is rich in sulphides, and these fuel lush colonies of chemosynthetic bacteria that oxidise the sulphides to synthesise complex organic molecules from carbon dioxide dissolved in the water. These organic molecules provide the nutritional resource for rich communities of diverse animals – including *R. exoculata* and *B. thermydron* – that depend on the vents for survival. Some speculate that the eyes of *R. exoculata* have evolved to see the infrared light resulting from the heat, thereby having a mechanism to orient themselves towards or away from the vent. However, no infrared-sensitive visual pigment has been found in these animals (or indeed in any animal), and infrared light is rapidly absorbed in water, severely limiting its useful range. Moreover, the only visual pigments isolated from the eyes of *R. exoculata* maximally absorb green light ($\lambda_{\text{max}} = 500 \text{ nm}$; van Dover *et al.*, 1989). For orientation towards or away from a hot vent, a simple temperature receptive organ would do a much better job.

Other possible sources of light include chemiluminescence, triboluminescence and sonoluminescence produced as the result of chemical interactions within the hot water plume gushing from the vent (White *et al.*, 2000; Reynolds & Lutz, 2001). These processes have the potential to produce an extremely weak visible light. Indeed, the highly sensitive naked-retina eyes of the vent crab *B. thermydron* (Land, 2002), which contain a visual pigment with peak sensitivity at 489 nm, may very well be able to see this light, allowing the crab to orient towards and away from the vent (Jinks *et al.*, 2002). However, just as in other parts of the deep ocean, the most likely source of light seen by vent crustaceans is that produced by other animals, although admittedly very little bioluminescence has ever been reported at hydrothermal vents (Marshall *et al.*, 1999).

IX. CONCLUSIONS

(1) The nature of the visual scenes viewed by marine animals changes dramatically with depth. In the

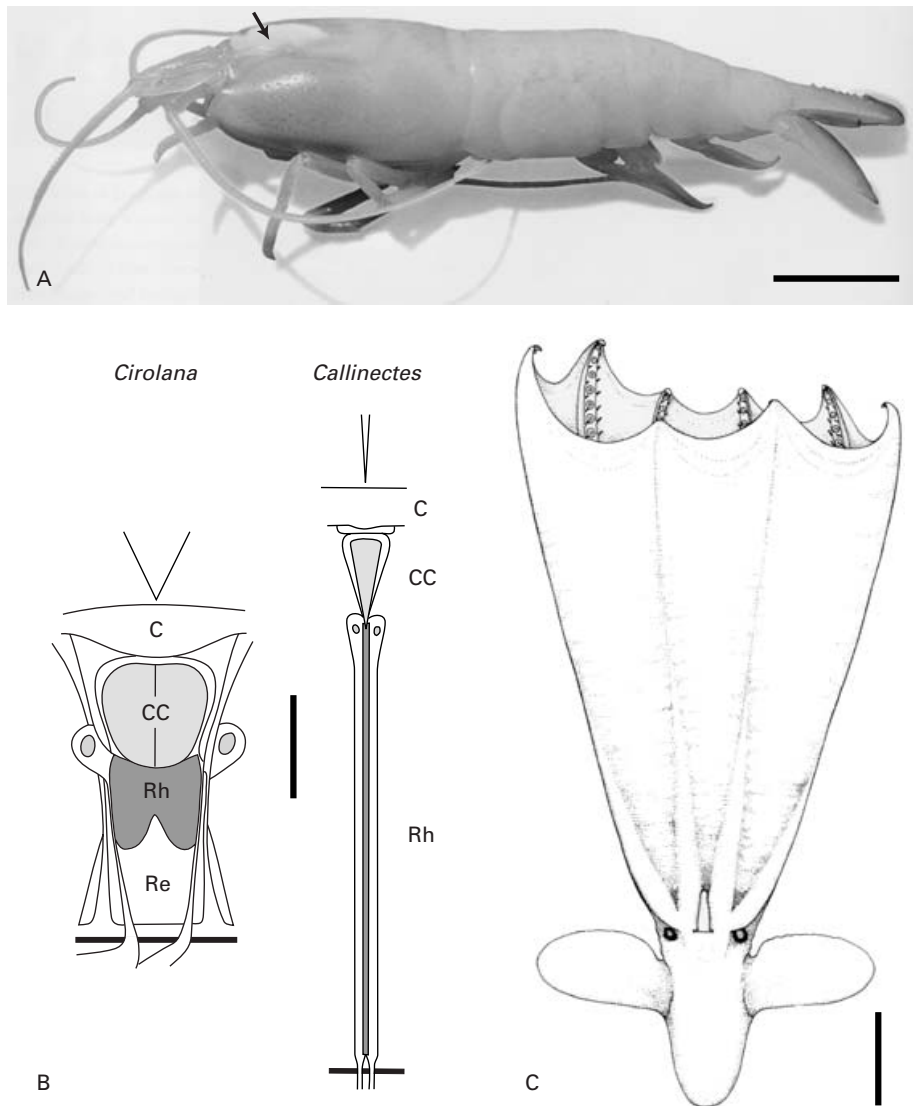


Fig. 16. Visual adaptations in benthic and benthopelagic invertebrates. (A) The bresiliid shrimp *Rimicaris exoculata*, which lives around hydrothermal vents at abyssal depths. Their eyes (arrow) consist of enlarged flattened sheets of naked rhabdoms. Scale bar = 10 mm. From Rice (2000). (B) Ommatidial structure in the benthic isopod *Cirolana borealis* (left) and the coastal crab *Callinectes ornatus* (right). Receptive fields, apertures and rhabdoms are much larger in the deep-living *Cirolana borealis*, an indication of the greater sensitivity of this eye (which is reinforced by the presence of a reflective pigment tapetum, Re). C, corneal facet lens; CC, crystalline cone; Rh, rhabdom. Scale bar = 100 μ m. After Land (1984a), using diagrams from Nilsson & Nilsson (1981) and Waterman (1981). (C) The benthopelagic deep-sea finned octopod *Cirrothauma murrayi*, which has a reduced visual system. Scale bar = 80 mm. From Aldred *et al.* (1983).

mesopelagic zone (150–1000 m), the extended daylight scene becomes dimmer, bluer and more dorsally downwelling with increasing depth, whilst pin-points of bioluminescence become increasingly prominent. In the bathypelagic zone (>1000 m), points of bioluminescence are the only lights that are visible. In benthic habitats, other animals are most likely to be encountered on and above the flat sea floor directly ahead, thus constraining the visual world in two dimensions.

(2) The eyes and vision of deep-sea animals inhabiting different depths are matched to this gradual change in visual scene from extended source to point source.

(3) Those from the mesopelagic zone have the most varied eye designs of the deep sea. Some eyes are designed for maximum sensitivity to the dim, extended, dorsally directed space light, and for breaking the various forms of camouflage that animals employ for concealing their silhouettes from below. Others are designed for maximising the detection of point-source bioluminescence, with the prevalence of this design increasing with increasing depth. Some animals even have separate areas of their retina designed for detecting both types of light.

(4) In the nutritionally impoverished bathypelagic zone, the eyes of marine animals are generally smaller than in the

mesopelagic zone. They are nevertheless sophisticated, being designed for accurate detection and interception of point-source flashes of bioluminescence at ecologically meaningful distances.

(5) In the nutritionally richer benthic zone marine eyes tend to be larger. Many fishes have retinas possessing horizontal 'visual streaks' of higher ganglion cell density that are matched to the flat horizontal world directly ahead where other animals, lit by daylight or bioluminescence, are likely to be encountered.

(6) It is not only the intensity of light at different depths, but also its distribution in space, which has been a major force in the evolution of deep-sea vision.

However, despite these conclusions, it would be smug indeed to suggest that we have fully solved Murray's and Hjort's puzzle. We haven't. Certainly the changing nature of visual scenes with depth – from extended to point source – would solve much of their dilemma. Despite this, there are numerous exceptions to new-found 'rules' and curious anomalies that continue to fascinate. These however only fuel an excitement for the beauty and mystery of the deep sea, our last natural frontier.

X. ACKNOWLEDGEMENTS

The authors would like to thank Drs Kerstin Fritsches, Peter Herring, Michael Land, Sönke Johnsen, Almut Kelber and Justin Marshall for critically reading the manuscript, and Drs Olle Munk, Sir Eric Denton, Dan-Eric Nilsson, Michael Land, Sönke Johnsen, Julian Partridge and Shaun Collin for graciously allowing us to use their previously published figures. E.J.W. is also extremely grateful to the Swedish Research Council and STINT for their ongoing support.

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XII. APPENDIX A: DERIVATION OF EQUATION (6)

Imagine a photoreceptor that is absorbing N_e photons during each integration time from the extended space

light of the surrounding ocean. Imagine also that a flash of point-source bioluminescence, equal in duration to the integration time of the photoreceptor, suddenly supplies N_p photons to the photoreceptor. For the two consecutive photon samples (N_e and $N_e + N_p$) to be distinguished from each other with 95 % reliability (Land, 1981*a*), then

$$N_p \geq 1.96 \sqrt{2(N_e + X)}, \quad (\text{A1})$$

where X is the dark noise rate in ‘false’ photons per second (see Section V). From equations (1) and (2) (Section V)

$$N_e = L_e S = L_e \left(\frac{\pi A d}{4f} \right)^2, \quad (\text{A2})$$

where L_e is the number of down-welling photons $\text{m}^{-2} \text{s}^{-1} \text{sr}^{-1}$ that are available from the surface for vision in an eye with peak sensitivity to blue (475 nm) light, S is the optical sensitivity of the eye, A is the diameter of the pupil, f is the focal length of the eye, and d is the diameter of the photoreceptor.

From equation (3) (Section V)

$$N_p = \frac{EA^2}{16r^2} e^{-\alpha r}, \quad (\text{A3})$$

where E is the total number of photons emitted by a point source of bioluminescence at source per second, r is the distance of the point source from the eye and α is the combined attenuation coefficient. Please note that the term $(1 - e^{-\alpha r})$ has been neglected in the present use of equations (1) and (3), that is, we are assuming for simplicity that all the light incident on the photoreceptor is absorbed by it: $(1 - e^{-\alpha r}) \approx 1$.

At threshold, $N_p = 1.96 \sqrt{2(N_e + X)}$. Squaring both sides we obtain:

$$N_p^2 = 7.68(N_e + X). \quad (\text{A4})$$

After substituting equations (A2) and (A3) into equation (A4), and rearranging for L_e , we obtain:

$$L_e = \left(\frac{4f}{\pi A d} \right)^2 \left[\left(\frac{EA^2 e^{-\alpha r}}{44.3r^2} \right)^2 - X \right]. \quad (\text{A5})$$

From Section III, we know that below a depth of 100 m, L_e declines by approximately 1.5 log units per 100 m of further depth, that is

$$L_e = L_o \cdot 10^{-0.015(D_u - 100)}, \quad (\text{A6})$$

where L_o is the number of down-welling photons $\text{m}^{-2} \text{s}^{-1} \text{sr}^{-1}$ at 100 m depth that are available from the surface from above (subscript u) for vision in an eye with peak sensitivity to blue (475 nm) light (approximately 6.8×10^{18} photons $\text{m}^{-2} \text{s}^{-1} \text{sr}^{-1}$: see Section III), and D_u is the depth in metres. Rearranging equation (A6),

we obtain

$$D_u = 100 - 66.7 \log_{10} \left[\frac{L_c}{L_o} \right], \quad (\text{A7})$$

and following substitution of equation (A5) we obtain equation (6):

$$D_u = 100 - 66.7 \log_{10} \left\{ \frac{1}{L_o} \left(\frac{4f}{\pi A d} \right)^2 \left[\left(\frac{E A^2 e^{-ar}}{44.3 r^2} \right)^2 - X \right] \right\}. \quad (6)$$

(a) *The transition to the bathypelagic zone*

At bathypelagic depths (below approximately 1000 m), insufficient daylight penetrates to be seen. The only limit to point-source detection then becomes the dark noise present in the photoreceptor. That is, for reliable threshold detection in the bathypelagic zone, $\mathcal{N}_p = 1.96\sqrt{2X}$ (equation 4, Section V). If we compare this expression with equation (A1) for mesopelagic detection, we can see that bathypelagic detection occurs at depths where $X \gg \mathcal{N}_c$. For an average fish eye, and $X = 0.0001$ ‘false photons’ s^{-1} , we will now show that this condition is satisfied for depths at and below approximately 1000 m.

From equations (A3) and (A5)

$$L_c = \left(\frac{4f}{\pi A d} \right)^2 \left[\frac{\mathcal{N}_p^2}{7.68} - X \right] \cong 2.8 \times 10^{11} \left[\frac{\mathcal{N}_p^2}{3.84 \cdot 2} - X \right], \quad (\text{A8})$$

where we have assumed a fish eye with $f = 1.25A$ (Matthiessen’s ratio) and rods of diameter $d = 3 \times 10^{-6}$ m. Equating equations (A6) and (A8), noting that L_o is 6.8×10^{18} photons $m^{-2} s^{-1} sr^{-1}$, and rearranging for \mathcal{N}_p , we obtain

$$\mathcal{N}_p = \sqrt{1.2 \times 10^8 \times 10^{-0.015(D_u - 100)} + 3.84 \cdot 2X}. \quad (\text{A9})$$

Equation (A9) reduces to the bathypelagic equation (4) ($\mathcal{N}_p = 1.96 \cdot \sqrt{2X}$) when the first term under the square root becomes much smaller than the second. At what depth D_u does this occur, when the first term becomes (say) 1 % of the second? That is, at what depth is the following condition satisfied?

$$1.2 \times 10^8 \times 10^{-0.015(D_u - 100)} = 0.01 \times 3.84 \cdot 2X.$$

With $X = 0.0001 s^{-1}$, $D_u = 980$ m. That is, for this average fish eye, bathypelagic point-source detection takes over from mesopelagic point source detection at a depth of approximately 1000 m.