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On the functions of double eyes in midwater animals

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Midwater predators often have double eyes consisting of a large upward-pointing part with a narrow field of view and high resolution, and a small downward-pointing part with a wide field of view and low resolution. In crustaceans with compound eyes the different eye parts are of basically similar construction, but in fishes the downward-pointing regions may employ unusual optical systems with unknown image-forming capabilities. It has been suggested that the upward-directed parts are used to detect silhouettes of animals against the residual daylight, whereas the lower parts look out for luminescent organisms. Here I calculate the sizes that apposition compound eyes would need to attain in order to fulfil these tasks, and the way that size should vary with depth. It is concluded that silhouette detection is much the more demanding task, and becomes increasingly difficult as light levels decrease. For this reason the upward-pointing parts must increase rapidly with depth. This is not the case with luminescence detectors, where the task is most difficult near the surface because of upwelling background light, and becomes easier with depth. On the whole these predictions fit well with the sizes and shapes of real midwater eyes, especially in the case of the hyperiid amphipods.

Keywords: amphipod; camouflage; deep sea; eye; luminescence; vision

1. INTRODUCTION

Many animals that live at depths between about 200 and 800 m are equipped with double eyes. At these depths the daytime light conditions vary between twilight and starlight, and the downwelling light is about 200 times brighter than the upwelling light. Double eyes are found in three phyla (vertebrates, crustaceans and molluscs), and in three optically different types of eye (single-chambered, apposition compound and refracting superposition). In all these diverse structures it is usually the upward-pointing component of the eye that is larger and has higher resolution. The smaller lower-eye component views the water below and to the side of the eye.

2. SURVEY

Amongst fishes the double nature of the eyes manifests itself as a large upward-pointing eye with a restricted field of view, and a second optical system of a very variable nature that projects an image of some kind onto an accessory retina or retinal diverticulum. In *Opisthoproctus grimaldii*, *Stylephorus chordatus* and *Dolichopteryx longipes* the accessory optical system appears to be a mirror (Collin *et al*. 1997; Locket 1977). In *Scopelarchus guntheri* and *Benthalbella infans* the optical device is a 'lens pad' made up of light-guiding plates that direct light from below via the lens to an accessory retina. *Evermannella* spp. have a similar structure but of different origin (Locket 1977). The downward-pointing component of the eye of *Bathylychnops exilis* has a separate lens formed from the sclera of the major eye (Locket 1977). In addition to the fishes with two distinct optical systems, there are many others (e.g. *Argyropelecus* spp.) that have only the upward-pointing component. The only example in a cephalopod mollusc of a similar optical division of labour is the very odd case of the squid *Histioteuthis*. Here there are two eyes, as usual, but one is large and tubular, and the other is smaller, with a wider field of view (photograph in Land (1981)). The photophore pattern indicates that the larger eye normally points upwards, and this is confirmed by the fact that it has a yellow lens, whereas the lens of the smaller eye is clear. It is believed that yellow lenses help to break the camouflage provided by downward-pointing photophores, especially when the colour of the emitted light does not quite match that of the residual daylight (Douglas & Marshall 1999).

Two crustacean groups have double eyes that show very similar trends with increasing depth, even though their optical systems differ fundamentally. In hyperiid amphipods that live near the ocean surface the apposition eyes tend to be small, single, with relatively small facets. Upper midwater animals (*Brachyscelus*, *Paraphronoe* and *Themisto* spp.) have larger eyes that are still physically single with a single retina, but with a distinct upper region of larger facets (see later, figure 2*a*). In other species (*Phrosina* and *Platyscelus* spp.) the two regions have separate retinas. *Phronima sedentaria* lives at greater depths (< 800 m), and here both eyes and retinas are separate. In the upper eye (see figure 2*a*) the radius of curvature is large (about 5 mm) as are the facets (diameter 150 μm), the interommatidial angles are very small (*ca*. 0.25°) and the field of view of the eye itself is tiny (*ca*. 10°). By contrast, the lower eye has small facets (80 μm), large interommatidial angles (*ca*. 10 μm) and a field of view of greater than 180° (Land 1989). The deepest-living hyperiid with a good eye is *Cystisoma*, which has no downward-pointing region, and an upward-pointing region with huge facets and a field of view of about 10°, much as in *Phronima*.

The euphausiids have refracting superposition eyes in which many facets contribute to each point on the image. Many have single spherical eyes, but in several genera (*Nematoscelis*, *Nematobrachion* and *Stylocheiron*) there are midwater species with double eyes. Again, the upper eyes have small fields of view, large facets and interreceptor angles that are typically about half those of the lower eyes (Land *et al.* 1979). Interestingly, there is a series of double-eyed *Stylocheiron* species that live in the surface waters, which have very small upper eyes; this seems to be a mechanism for restricting the size of the superposition pupil in an environment where there is plenty of light. However, in midwater species the upper and lower eyes are of similar size, and in *Nematobrachion boopis* the lower eye is reduced to the point of being almost rudimentary, reminiscent of the hyperiid *Cystisoma*.

3. POSSIBLE FUNCTIONS

At first sight it seems peculiar that in all the double-eyed groups the upward-pointing eye region, which views the surface, should be so much bigger—and better—than the part of the eye that looks below the animal. If both parts were doing similar jobs, then the lower part would need to be much bigger than the upper, to compensate for the 2–3 log-unit difference in background luminance. Eye size can be 'spent' on resolution or sensitivity, and because the downward-pointing components always have lower resolution than the upper, it is still possible that they have increased sensitivity. Calculations on hyperiid eyes indicate that the sensitivity to extended sources is, on average, about twice as great for the lower components compared with the upper. This is still nowhere near adequate to cope with the difference in background luminance. We therefore have to conclude that whatever the upper eyes are doing, the lower ones are doing something different.

Such evidence as there is strongly suggests that upper eyes look into the residual daylight from the sea surface. At midwater depths the possible diets are restricted to falling detritus such as faeces and skeletal remains, or other animals. The latter are generally countershaded from above and camouflaged with mirrors from the side, and so can often only be seen below as a silhouette against the downwelling light. Even then, the almost universal trick of 'luminous countershading' with photophores can, if accurately controlled, obliterate the silhouette when viewed from a distance. All this argues for high resolution, so that small disturbances in the light-field caused by opaque objects can be detected at large distances, and high sensitivity so that small contrast differences can be detected at low light levels. It seems certain from their positions in the head that the tubular eyes of fishes do point upwards, and there is direct evidence that the upper components of the double eyes of euphausiids are kept pointing upward by a dorsal light reflex (Land 1980). However, the postures of swimming hyperiids seem to be rather more variable (Land 1992).

What then are the downward-pointing eye components doing? The only other source of light in the sea is the bioluminescence of other creatures, and presumably this is what the lower eyes are trying to detect. No other conclusion seems possible. This is essentially a bright-source detection task where a single photon can be taken as evidence of bioluminescence, if the retina is noise-free, and this is far less demanding than the upper eye task of detecting a local reduction in the numbers of photons. In the hyperiid amphipod *Phrosina semilunata* there is direct behavioural evidence that the animals track self-luminous objects using the lower eyes (Land *et al.* 1995).

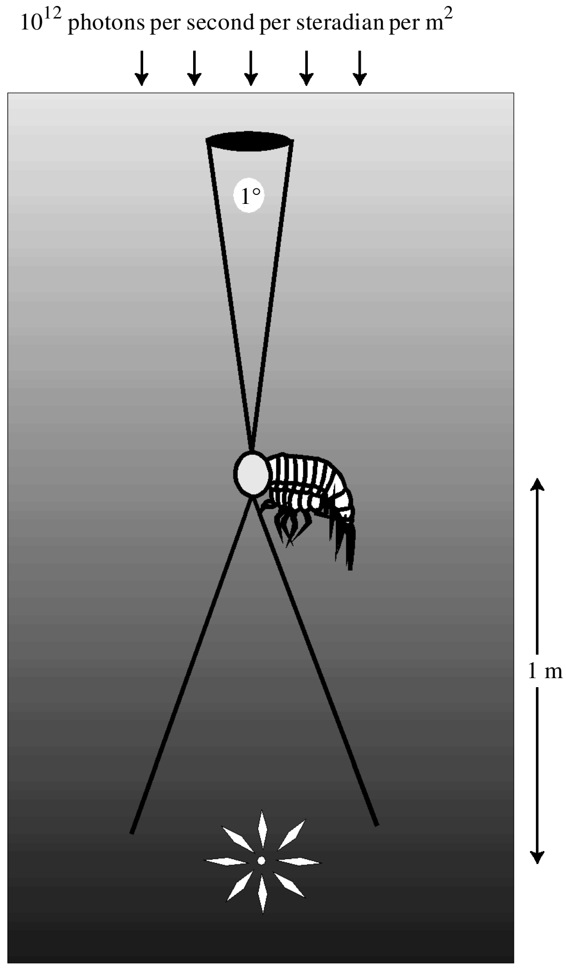

Figure 1. Proposed tasks for upward- and downward-pointing eyes. Details in § 4.

The two calculations that follow are essentially feasibility studies intended to provide realistic 'designs' for eyes that can perform the two distinct functions of detecting dark objects against a dim background, and detecting self-luminous organisms. The intention is to compare these predictions with the absolute and relative sizes of the eye components of real midwater animals.

4. CALCULATIONS OF REQUIRED EYE SIZE

(a) *Looking upwards: darker objects against a dim background*

A realistic task for such an eye would be to detect a 1° opaque object (e.g. 1 cm at 57.3 cm) at 500 m depth (figure 1). First I calculate how many photons are needed

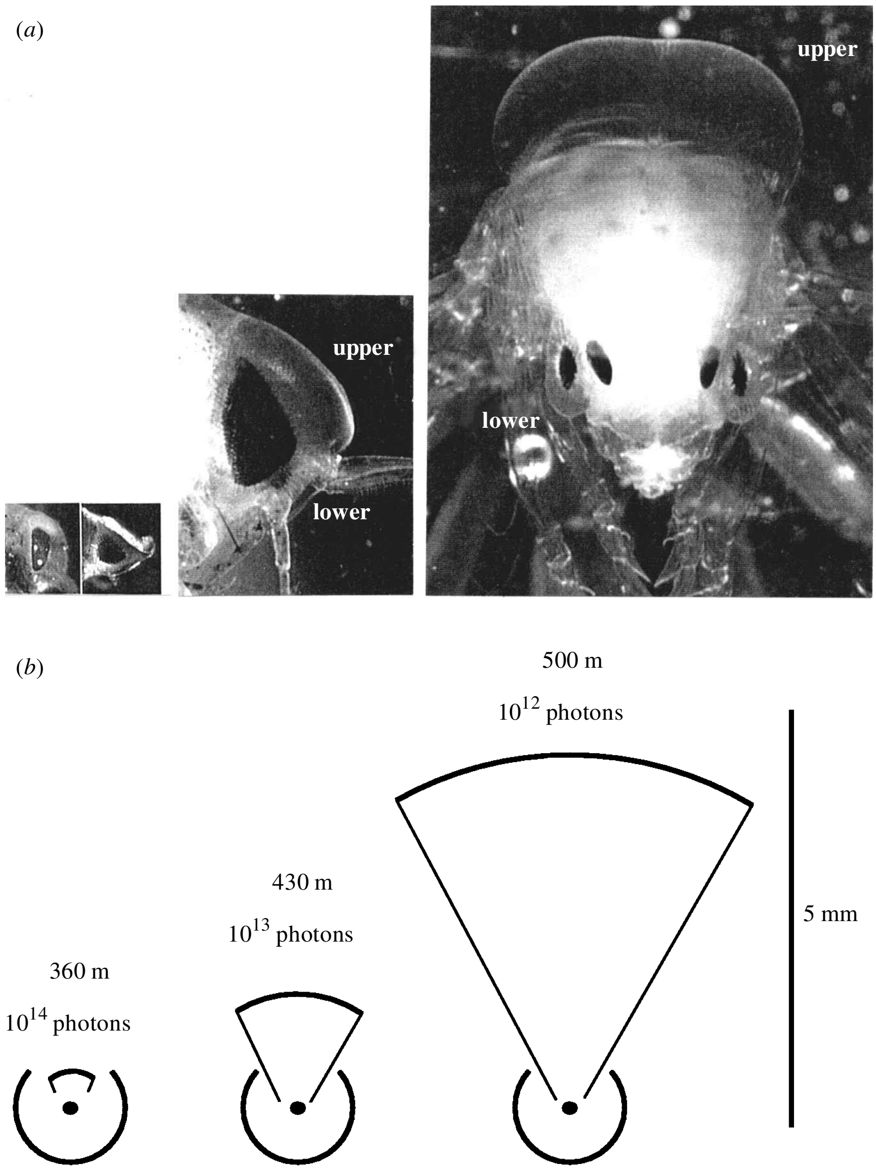

Figure 2. (*a*) The eyes of hyperiid amphipods from three different depth ranges, magnified to the same absolute size. Left, two animals from the top 100 m (*Lestrigonus* sp. and *Thamneus* sp.); middle, *Themisto compressa* from the upper mid-water (< 300 m); right, *Phronima sedentaria* whose range extends down to 800 m. Note the great increase in size of the upward-pointing eye region with increasing depth. (*b*) Calculated eye radii for apposition compound eyes capable of fulfilling the tasks shown in figure 1, at different depths. The photon numbers refer to the residual skylight, and the full units are photons per steradian per square metre per second. Fields of view of the upper eyes have been restricted arbitrarily to 60°. Note the overall similarity in absolute size to the animals in (*a*), and the relative increase in size of the upper part with increasing depth. The 5 mm scale on (*b*) also applies to (*a*).

for the task, and second how many are made available by eyes of different sizes. The calculations are done for an apposition compound eye (e.g. the eye of an amphipod), but are easy to adapt for other types of eye. The general methods are described in Land (1981).

The Poisson statistics of photon fluctuations mean that the detectability of a difference in photon numbers is proportional to the square root of mean photon number in each time sample. This leads to a version of the Rose–DeVries law: the number of photons required to detect a given contrast is equal to $1/(\text{contrast})^2$. For an opaque object the contrast (C) is 1, so one photon is needed per receptor per integration time. If the contrast were reduced to 10%, 100 photons would be needed. (These calculations assume that the retina has insignificant 'dark noise'.)

How many photons are available to receptors? The sensitivity of an eye (S) is the ratio of the number of photons received by a receptor to those emitted by the surface it is imaging. For monochromatic light this is given by

$$S = (\pi/4)^2 A^2/f^2 d^2 (1 - e^{-kx}), \tag{1}$$

where A is the aperture diameter, f the focal length, d the receptor diameter, k the absorption coefficient of the photopigment and x the photoreceptor length. As the acceptance angle of a photorecetor $(\Delta\rho) \approx d/f$, the formula can be rewritten as

$$S = (\pi/4)^2 A^2 \Delta\rho^2 (1 - e^{-kx}). \tag{2}$$

The number of photons absorbed (N) is given by $N = S/L$, where L is the source luminance in photons per second per steradian per square metre. At 500 m in clear water at midday L is about 10^{12}. If we make $N = 1$ (i.e. contrast of 1), $S = 1/L$ and equation (2) becomes

$$1/L = (\pi/4)^2 A^2 \Delta\rho^2 (1 - e^{-kx}). \quad (3)$$

Assuming $\Delta\rho = 1°$ (0.0175 radians (rad)) and $(1 - e^{-kx}) = 1$ (i.e. all photons absorbed), $A = 72.8$ µm (contrast of 1). This is quite large for a compound eye, but fairly typical of midwater hyperiids. The interommatidial angle ($\Delta\phi$) in a spherical apposition eye is equal to A/R (rad), where R is the eye radius. Then if $\Delta\phi = \Delta\rho = 1°$, the radius of curvature of the eye will be 4.2 mm (figure 2*b*). However, if the contrast of the object is reduced to 0.1, or the animal lived 140 m deeper (100 times less light in clear ocean water) the required aperture would increase tenfold to 728 µm, and the eye radius to 42 mm, which is not possible on a 10 mm animal. Reducing the sampling time of the retina from the 1 s assumed here to 0.1 s would be equivalent to a 70 m increase in depth.

(b) *Looking downwards: flashing objects on a dark background*

The task set for the downward-pointing eye is to detect a flashing copepod at a distance of 1 m (figure 1). Photon statistics are almost irrelevant to this task. If a photon is detected it presumably came from an organism. According to Peter Herring (personal communication) a typical flash emission (E) from a copepod provides a total of 10^{11} photons. As this is spread over $4\pi r^2$ m^2, the number of photons (N) passing through a square metre at a distance r is given by

$$N = E/4\pi r^2. \quad (4)$$

If $E = 10^{11}$ photons, and $r = 1$ m, $N = 8 \times 10^9$ m, or 0.008 µm. From the latter figure, the surface area required to detect, on average, one photon, will be 1/0.008, or 126 µm^2. This corresponds to a circular detector with a diameter (A) of $2\sqrt{(126/\pi)}$, i.e. $A = 12.7$ µm. This is very small for an ommatidial facet. The angle over which such a detector collects is not set by the physics of the situation (unlike the upward-pointing task), but by the extent to which an organism needs to discriminate direction. If it intends to prey upon luminous organisms then this needs to be fairly good, perhaps a degree or two, but if it merely needs to detect the presence of luminescence it could be 10° or more. Even with 1° resolution, a compound eye for detecting luminescing animals at 1 m would only have a radius of 0.72 mm; about one-sixth that of an upward-pointing dark-object detector (figure 2*b*).

The detectability of luminescent objects decreases at shallower depths where there is sufficient upwelling light for photon noise to compete with the luminescent signal. Equation (3) can be used to calculate the luminance at which this occurs, and this corresponds to a daylight depth of about 350 m. The signal-to-background ratio can be improved by decreasing the ommatidial acceptance angles (so that they 'see' less background), and this leads ultimately to an eye that does not differ from the upward-pointing eye. Hence, perhaps, the lack of specialization in eyes from the top 100 m (figure 2*a*).

5. CONCLUSIONS

The calculations confirm that detecting objects against dim downwelling light is a demanding task requiring large eyes. For apposition eyes the task begins to become unrealistic somewhere around the middle of the mesopelagic range (*ca.* 500 m). For eyes of the superposition and single-chambered type, which are intrinsically more sensitive, the same conclusions hold, although the depth at which upward vision becomes impracticable may be as much as 200 m deeper. It also emerges that decreasing the contrast of the object relative to the background makes it far more difficult to see; if the contrast is reduced from 100% to 10%, 100 times more light is required, necessitating a ten-times larger eye. Clearly even a fairly inefficient counter-illumination camouflage system will convey great protection.

Eyes for detecting light from bioluminescent flashes against a dark background can be quite small, and this is consistent with the small size of most downward-pointing eye components. It is interesting that in many cases the resolution is poor (e.g. 10° acceptance angles in *Phronima*, and probably worse with some of the strange optical arrangements in fishes). This implies that the bearers of these eyes are not particularly concerned with knowing the exact direction of the luminescent objects for predation purposes, but they do, nevertheless, want to know about their presence.

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