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On the functions of double eyes
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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 do 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 crus 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 crus 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 construc-
tion, but in 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 capabil tion, 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 a 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 c 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 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 m 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 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 lumines-
cence detectors, whe reason the upward-pointing parts must increase rapidly with depth. This is not the case with lumines-
cence detectors, where the task is most difficult near the surface because of upwelling background light,
and becomes ea cence 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 ey

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

1. INTRODUCTION

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

Amongst fishes the double nature of the eyes manifests EXECT

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 ontical system of a very vari-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 vari-
able nature that projects an image of some kind onto itself as a large upward-pointing eye with a restricted
field of view, and a second optical system of a very vari-
able nature that projects an image of some kind onto an
accessory retina or retinal diverticulum. In Objsth 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 *Opisthop roctus* grimaldii. Stylet harves chardatus and *Delich* able nature that projects an image of some kind onto an accessory retina or retinal diverticulum. In *Opishop roctus grimaldii*, *Stylephorus chordatus* and *Dolichopteryx longipes* the accessory optical system appears t 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 *Scobe 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 devi 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 *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 *Fremann 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 origi 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 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 eximilar 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 t 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 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.

Argyrop elecus spp.) that have only the upward-pointing
component The only example in a cephalopod mollusc of *Argyropelecus* spp.) that have only the upward-pointing component. The only example in a cephalopod mollusc of a similar ontical division of labour is the very odd case of *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 Histoteuthis. Here there are two every 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, 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 L but one is large and tubular, and the other is smaller, The photophore pattern indicates that the larger eye 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 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 eve is clear. It is believed that vellow lenses hel 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-pointi 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 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 dayl 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) photophores, especially when
light does not quite match the
(Douglas & Marshall 1999).
Two crustacean groups ha light does not quite match that of the residual daylight (Douglas & Marshall 1999).
Two crustacean groups have double eyes that show

(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 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 very similar trends with increasing depth, even though
their optical systems differ fundamentally. In hyperiid
amphipods that live near the ocean surface the apposition
eves tend to be small, single, with relatively small 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.
Unner midwater animals (Brachyscelus Parahranee amphipods that live near the ocean surface the apposition
eyes tend to be small, single, with relatively small facets.
Upper midwater animals *(Brachyscelus, Parapronoe* and
Themisto spp) have larger eyes that are still eyes tend to be small, single, with relatively small facets.
 Themisto spp.) have larger eyes that are still physically
 Themisto spp.) have larger eyes that are still physically

single with a single retina but with a Upper midwater animals (Brachyscelus, Parapronoe 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 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
senarate retinas *Phronima sedentaria* live 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 eves and r 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 2a) the 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 fac (\leq 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 intercommatidial angles are very small 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 $(ca. 0.25^{\circ})$ and the field of view of the eye itself is tiny large (about 5 mm) as are the facets (diameter 150 μ m), the interommatidial angles are very small (*ca.* 0.25°) and the field of view of the eye itself is tiny (*ca.* 10°). By the interommatidial angles are very small $(\alpha a. 0.25^{\circ})$ and
the field of view of the eye itself is tiny $(\alpha a. 10^{\circ})$. By
contrast, the lower eye has small facets $(80 \,\mu\text{m})$, large
interommatidial angles $(\alpha, 10 \,\mu\text$ the field of view of the eye itself is tiny $(ca. 10^{\circ})$. By
contrast, the lower eye has small facets $(80 \,\mu\text{m})$, large
interommatidial angles $(ca. 10 \,\mu\text{m})$ and a field of view of
greater than 180° (I and 1989). The contrast, the lower eye has small facets (80 μ m), large
interommatidial angles (ca. 10 μ m) and a field of view of
greater than 180° (Land 1989). The deepest-living

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TRANSACTIONS $\overline{\overline{O}}$ hyperiid with a good eye is *Cystisoma*, which has no
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° , 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 supe

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 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 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 inter (*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 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 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-eved *Stylocheiron* species that live 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: (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 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 rudime However, in midwater species the upper and lower eyes are of similar size, and in *Nematobrachion boop is* the lower eye is reduced to the point of being almost rudimentary, reminiscent of the hyperiid *Cystisoma*. are of similar size, and in *Nematobrachion* boop is the lower

3. POSSIBLE FUNCTIONS

At first sight it seems peculiar that in all the double-eyed 3. POSSIBLE PONCTIONS
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 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 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 nee 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 th 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. E 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 be 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-nointing components always have lower res 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 resolu-
tion than the upper it is still possible that they 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 downward-pointing components always have lower resolution than the upper, it is still possible that they have
increased sensitivity. Calculations on hyperiid eyes indi-
cate that the sensitivity to extended sources is on a tion than the upper, it is still possible that they have
increased sensitivity. Calculations on hyperiid eyes indi-
cate that the sensitivity to extended sources is, on average,
about twice as great for the lower component 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 unner This is still nowhere near adequa cate 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 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 eves are 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 with the difference in background luminance. V
have to conclude that whatever the upper eyes
the lower ones are doing something different.
Such evidence as there is strongly suggests Such evidence that whatever the upper eyes are doing,
Such evidence as there is strongly suggests that upper
es look into the residual daylight from the sea surface

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 denths the possible diets are restricted to 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 faces and skeletal remains 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 countersha At midwater depths the possible diets are restricted to as evidence of bioluminescence, if the retina is noise-free, falling detritus such as facces and skeletal remains, or and this is far less demanding than the upper ey falling detritus such as facces 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 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 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 photoand 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 silhouuniversal trick of 'luminous countershading' with photo-
phores can, if accurately controlled, obliterate the silhou-
ette when viewed from a distance. All this argues for high
resolution, so, that small, disturbances, in phores 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 l ette 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 bigh sensitivity so that small contrast 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 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 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 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 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 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 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 euphausiids are kept pointing upward by a dorsal lightreflex (Land 1980). However, the postures of swimming hyperiids seem to be rather more variable (Land 1992). What then are the downward-pointing eye component Hex (Land 1980). However, the postures of swimming
periids seem to be rather more variable (Land 1992).
What then are the downward-pointing eye components
ing? The only other source of light in the sea is the

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 *Phil. Trans. R. Soc. Lond.* B (2000)

 10^{12} photons per second per steradian per m²

 10^{11} photons

Figure 1. Proposed tasks for upward- and downward-pointing
eves Details in 8.4 Figure 1. Proposed t
eyes. Details in §4.

bioluminescence of other creatures, and presumably this
is what the lower eyes are trying to detect. No other 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 brightbioluminescence 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 take 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 biolyminescence if the retina is noiseconclusion 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 e 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 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 hyneriid amphinod *Phrosina semilynata* t 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 eves (I and *et al.* 1 the hyperiid amphipod *Phrosina semilunata* ther
behavioural evidence that the animals track sell
objects using the lower eyes (Land *et al.* 1995).
The two calculations that follow are essenti havioural evidence that the animals track self-luminous
jects using the lower eyes (Land *et al.* 1995).
The two calculations that follow are essentially feasi-
ity studies intended to provide realistic 'designs' for eyes

bijects using the lower eyes (Land *et al.* 1995).
The two calculations that follow are essentially feasi-
bility studies intended to provide realistic 'designs' for eyes The two calculations that follow are essentially feasi-
bility studies intended to provide realistic 'designs' for eyes
that can perform the two distinct functions of detecting
dark objects against a dim background and det bility 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 com 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 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) *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 Leakulate bow many photon 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

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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 (*Lestringnus* sp. and *Themeus* sp.): middle. *Themista combressa* 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* 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* 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 i 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 a 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 ar 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° metre per secon
size to the anim
applies to (*a*).

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

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 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 Rosethe 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 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 pe 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 given contrast is equal to $1/(\text{contrast})^2$. For an opaque pigment and object the contrast (C) is 1, so one photon is needed per angle of a preceptor per integration time. If the contrast were reduced rewritten as to 10%, 100 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 'dar receptor per integration time. If the contrast were redu
to 10%, 100 photons would be needed. (These calculat
assume that the retina has insignificant 'dark noise'.) *Phil. Trans. R. Soc. Lond.* B (2000)

How many photons are available to receptors? The sensitivity of an eye (S) is the ratio of the number of 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 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 photons recompressurface it is
given by

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

 $S = (\pi/4)^2 A^2/f^2 d^2 (1 - e^{-kx}),$ (1)
where *A* is the aperture diameter, *f* the focal length, *d* the
receptor diameter *k* the absorption coefficient of the photowhere A is the aperture diameter, f the focal length, d the receptor diameter, k the absorption coefficient of the photo-
pigment and x the photoreceptor length. As the acceptance receptor diameter, *k* the absorption coefficient of the photo-
pigment and *x* the photoreceptor length. As the acceptance receptor diameter, *k* the absorption coefficient of the photo-
pigment and *x* the photoreceptor length. As the acceptance
angle of a photorecetor $(\Delta \rho) \approx d/f$, the formula can be
rewritten as pigment and x
angle of a ph
rewritten as

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

BIOLOGICAL
SCIENCES

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TRANSACTIONS $\overline{0}$

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

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

 $1/L = (\pi/4)^2 A^2 \Delta \rho^2 (1 - e^{-kx}).$ (3)
Assuming $\Delta \rho = 1^\circ$ (0.0175 radians (rad)) and $(1-e^{-kx}) = 1$
(i.e. all photons absorbed) $A = 72.8$ um (contrast of 1) (i) $\frac{1}{\sqrt{1-\frac{1}{c}}}$ (i.e. all photons absorbed), $A = 72.8 \text{ }\mu\text{m}$ (contrast of 1).
This is quite large for a compound even but fairly typical (i.e. all photons absorbed), $A = 72.8 \,\mu\text{m}$ (contrast of 1).
This is quite large for a compound eye, but fairly typical of midwater hyperiids. The interommatidial angle $(\Delta \phi)$ 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^{\$ 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 $\Delta \phi = \Delta \rho = 1^{\circ}$, the radius of
curvature of the eve will be 4.2 mm (fi in a spherical apposition eye is equal to A/R (rad), where R is the eye radius. Then if $\Delta \phi = \Delta \rho = 1^{\circ}$, the radius of curvature of the eye will be 4.2 mm (figure 2*b*). However, if the contrast of the object is red *R* is the eye radius. Then if $\Delta \phi = \Delta \rho = 1^{\circ}$, 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 curvature of the eye will be 4.2 mm (figure $2b$). 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 inc 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 eve radius to 42 mm whi ocean water) the required aperture would increase
tenfold to $728 \mu m$, and the eye radius to $42 \, mm$, which is ocean water) the required aperture would increase
tenfold to $728 \mu m$, 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 1s assumed here to 0.1s wo tenfold to $728 \mu m$, 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 1s assumed here to 0.1s would
be equivalent to a 70 m increase in d not possible on a 10 mm animal. Reducing
time of the retina from the 1s assumed here
be equivalent to a 70 m increase in depth. **(b)** *Looking downwards: £ashing objects on a dark*

background

The task set for the downward-pointing eye is to detect **background**
The task set for the downward-pointing eye is to detect
a flashing copepod at a distance of 1m (figure 1). Photon
statistics are almost irrelevant to this task. If a photon is 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 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. Accord-
ing to Peter Herring (personal communication) a statistics are almost irrelevant to this task. If a photon is
detected it presumably came from an organism. Accord-
ing to Peter Herring (personal communication) a typical
flash emission (E) from a copepod provides a tot 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 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 photons. As this
photons (N) pass r is given by

$$
\mathcal{N} = E/4\pi r^2. \tag{4}
$$

 $N = E/4\pi r^2$. (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, If $E = 10^{11}$ photons, and $r = 1$ m, $\mathcal{N} = 8 \times 10^9$ m, or 0.008 μ m.
From the latter figure, the surface area required to detect,
on average, one photon, will be 1/0.008, or 126 μ m². This From the latter figure, the surface area required to detect,
on average, one photon, will be $1/0.008$, or $126 \mu m^2$. This
corresponds to a circular detector with a diameter (*A*) of
 $2./(126/\pi)$ i.e. $A = 12.7 \text{ µm}$. Thi corresponds to a circular detector with a diameter (A) of $2\sqrt{(126/\pi)}$, i.e. $A = 12.7 \,\mu\text{m}$. This is very small for an average, one photon, will be $1/0.008$, or $126 \mu m^2$. This
responds to a circular detector with a diameter (*A*) of
 $(126/\pi)$, i.e. $A = 12.7 \mu m$. This is very small for an
matidial facet. The angle over which such a dete ommatidial facet. The angle over which such a detector $2\sqrt{(126/\pi)}$, i.e. $A = 12.7 \,\mu\text{m}$. 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 unward-pointing task) but by the exten 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 in 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
prev upon luminous organisms then this needs t 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 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
de detect the presence of luminescence it could be 10° or
more. Even with 1° resolution, a compound eye for
detecting luminescing animals at 1m would only have a
radius of 0.72 mm; about one-sixth that of an unward 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-
nointing dark-object detector (figure $2b$) 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 pointing dark-object detector (figure $2b$).
The detectability of luminescent objects decreases at shallower depths where there is sufficient upwelling light for photon poise to compete with the luminescent signal 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 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 daylig 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
denth of about 350 m. The signal-to-background ratio 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 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 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 unward-pointing eye. Hence, perhaps, the lack of the upward-pointing eye. Hence, perhaps, the lack of specialization in eyes from the top 100 m (figure $2a$). this leads ultimately to an eye that does not differ f
the upward-pointing eye. Hence, perhaps, the lacl
specialization in eyes from the top 100 m (figure 2*a*).

5. CONCLUSIONS

The calculations confirm that detecting objects against The calculations confirm that detecting objects against
dim downwelling light is a demanding task requiring
large eves For annosition eves the task hegins to become 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 mesodim downwelling light is a demanding task requiring
large eyes. For apposition eyes the task begins to become
unrealistic somewhere around the middle of the meso-
pelagic range $(a-500 \text{ m})$. For eyes of the superposition large eyes. For apposition eyes the task begins to become
unrealistic somewhere around the middle of the meso-
pelagic range (*ca.* 500 m). For eyes of the superposition
and single-chambered type which are intrinsically mo unrealistic somewhere around the middle of the meso-
pelagic range $(aa. 500 \text{ m})$. For eyes of the superposition
and single-chambered type, which are intrinsically more
sensitive the same conclusions hold although the den pelagic range $(aa. 500 \text{ m})$. For eyes of the superposition
and single-chambered type, which are intrinsically more
sensitive, the same conclusions hold, although the depth
at which unward vision becomes impracticable may 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 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 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 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 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 makes it far more difficult to see; if the contrast is reduced from 100% to 10% , 100 times more light 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 required, necessitating a ten-times
even a fairly inefficient counter-illun
system will convey great protection.
Eves for detecting light from his even a fairly inefficient counter-illumination camouflage
system will convey great protection.
Eyes for detecting light from bioluminescent flashes

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 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
eve components. It is interesting that in many cases t 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 appl 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 op 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 eves are not particularly concerned wi 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 predaarrangements in fishes). This implies that the bearers of these eyes are not particularly concerned with knowing the exact direction of the luminescent objects for predathese eyes are not particularly concerned with knowing
the exact direction of the luminescent objects for preda-
tion purposes, but they do, nevertheless, want to know
about their presence the exact direction of
tion purposes, but the
about their presence.

REFERENCES

- **REFERENCES**
Collin, S. P., Hoskins, R. J. & Partridge, J. C. 1997 Tubular eyes
of deen-sea fishes: a comparative study of retinal topography of deep-sea fishes: a comparative study of retinal topography.
Brain Behan-Final 50, 335–357 *Brain Behav. Brain Behav. Evol.* 50, 335–357.
 Brain Behav. Evol. 50, 335–357.

puglas R. H. & Marshall N. 1 ofdeep-sea fishes: a comparative study of retinal topography.
 Brain Behav. Evol. 50, 335–357.

Douglas, R. H. & Marshall, N. J. 1999 A review of vertebrate

and invertebrate ocular filters. In *Adobtive mechanisms* in
- Brain Behav. Evol. 50, 335–357.

puglas, R. H. & Marshall, N. J. 1999 A review of vertebrate

and invertebrate ocular filters. In *Adaptive mechanisms in the*

ecology of vision (ed. S. N. Archer, M. B. A. Diamgoz, E. R. *ecology of vision* (ed. S. N. J. 1999 A review of vertebrate and invertebrate ocular filters. In *Adaptive mechanisms in the ecology of vision* (ed. S. N. Archer, M. B. A. Djamgoz, E. R. Loew J. C. Partridge & S. Valler and invertebrate ocular filters. In Adaptive mechanisms in the ecology of vision (ed. S. N. Archer, M. B. A. Djamgoz, E. R. Loew, J. C. Partridge & S. Vallerga), pp. 95–162. Dordrecht, The Netherlands: Kluwer ecology of vision (ed. S. N. A
Loew, J. C. Partridge & S.
The Netherlands: Kluwer.
and M. E. 1980. Eve mov Loew, J. C. Partridge & S. Vallerga), pp. 95–162. Dordrecht,
The Netherlands: Kluwer.
Land, M. F. 1980 Eye movements an[d the mechanism of](http://gessler.ingentaselect.com/nw=1/rpsv/cgi-bin/linker?ext=a&reqidx=/0340-7594^28^29137L.255[aid=536342,springer=1])
vertical steering in euphausiid crustages. $\frac{7 \text{ Camb} \quad Physical}$ 137
- The Netherlands: Kluwer.
und, M. F. 1980 Eye movements and the mechanism of
vertical steering in euphausiid crustacea. *J. Comp. Physiol*. **137**,
255–265. verticalsteering in euphausiid crustacea. *J. Comp. Physiol.* 137,
255–265.
Land, M. F. 1981 Optics and vision in invertebrates. In
Handhook of sensors hhysiology yol VIL/6B (ed. H.-L. Autrum)
- *Handbook of sensory physiology*, vol. VII/6B (ed. H.-J. Autrum), Handbook of sensory physiology, vol. VII/6B (ed. H.-J. Autrum), pp. 471-592. Berlin: Springer. Handbook of sensory physiology, vol. VII/6B (ed. H.-J. Autrum),
pp. 471–592. Berlin: Springer.
Land, M. F. 1989 The eyes of hyperiid amphipods: relations of
ontical structure to denth. 7 Camb. Physiol. A 164. 751–762
- pp. 471–592. Berlin: Springer.
und, M. F. 1989 The eyes of hyperiid amphipods: relations
optical structure to depth. *J. Comp. Physiol.* A 164, 751–762.
und M. F. 1992 I ocomption and visual behaviour of midwate Land,M. F. 1989 The eyes of hyperiid amphipods: relations of optical structure to depth. *J. Comp. Physiol.* A 164, 751-762.
Land, M. F. 1992 Locomotion and visual behaviour of midwater crustageans $\frac{7}{4}$ Mar Righ Ass
- optical structure to depth. *J. Comp. Physiol.* A 164, 751-762.
Land, M. F. 1992 Locomotion and visual behaviour of midwater
crustaceans. *J. Mar. Biol. Assoc. UK* 72, 41-70.
Land, M. F., Burton, F. A. & Meyer-Rochow, V. B Land,M. F. 1992 Locomotion and visual behaviour of midwater
crustaceans. *J. Mar. Biol. Assoc. UK* 72, 41–70.
Land, M. F., Burton, F. A. & Meyer-[Rochow, V. B. 1979 The](http://gessler.ingentaselect.com/nw=1/rpsv/cgi-bin/linker?ext=a&reqidx=/0340-7594^28^29130L.49[aid=536345,springer=1])
ontical geometry of euphausiid eyes. 7 Camb. Physiol
- optical geometry of euphausiid eyes. *J. Comp. Physiol.* **¹³⁰**, 49^62. opticalgeometry of euphausiid eyes. \tilde{J} . Comp. Physiol. 130, 49-62.
Land, M. F., Marshall, N. J. & Diebel, C. 1995 Tracking of blue lights by byperiid amphipods. \tilde{J} . Mar, Biol. Assoc. UK , 75
- 49–62.
und, M. F., Marshall, N. J. & Diebel, C. 1995 Tracking of
blue lights by hyperiid amphipods. *[J. Mar. Biol. Assoc. UK](http://gessler.ingentaselect.com/nw=1/rpsv/cgi-bin/linker?ext=a&reqidx=/0025-3154^28^2975L.71[aid=536346,csa=0025-3154^26vol=75^26iss=1^26firstpage=71])* **75**,
71–81. bluelights by hyperiid amphipods. \tilde{J} . Mar. Biol. Assoc. UK 75, 71-81.
- *Handbook of sensory physiology*, vol. VII/5 (ed. F. Crescitelli), pp. Handbook of sensory physiology, vol. VII/5 (ed. F. Crescitelli), pp.