The physical basis of reflective communication between fish, with special reference to the horse mackerel, *Trachurus trachurus*

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The physical basis for reflective communication between fish, with special reference to the horse mackerel, *Trachurus trachurus*

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SUMMARY

Some properties of reflecting structures in the external surfaces of *Trachurus trachurus* and some other fish are described. These are related to the hypothesis that such structures are useful, especially to schooling fish, for communicating information on relative positions, orientations, and movements between neighbours. In addition to the silvery layers on the main body surfaces, there are: (*a*) highly silvered patches on the tail, the pectoral fins and the jaws which, in the sea, will become much brighter or darker with any movement such as a tailbeat or mouth opening which changes their orientations in the ambient lightfield, and (*b*) structures such as the dorsal lateral line which, in the sea, will only appear bright from certain directions. To us, the colours of the ventral flanks change from bright red to blue with direction of viewing. These changes are given by two superposed layers of reflecting platelets which differ in their orientations and have spectral reflectivity curves close to those predicted by A. F. Huxley for interference reflectors which are 'ideal' $\lambda/4$ stacks of guanine crystals and cytoplasm. The wavebands best reflected by such platelets move to shorter wavelengths with increasing angle of incidence, also in accord with these equations. At normal incidence, the outer layer of platelets reflects maximally for far-red light which penetrates only a short distance in the sea. Such layers can, however, be useful at oblique angles where they reflect maximally in the yellow and blue. The inner layer of reflectors reflects very strongly in the blue at normal incidence, but reflects in the ultra-violet at oblique angles. Some theoretical studies are made on the ways in which the patterns of reflectivity by single and superposed layers of $\lambda/4$ stacks could signal a fish's movements or its position relative to its neighbours.

1. INTRODUCTION

(*a*) *Earlier work*

The external surfaces of many fish reflect visible light strongly, the reflecting elements being vast numbers of tiny platelets, each of which consists of a stack of thin, flat guanine crystals, separated by cytoplasm (Denton 1970). The optical properties of such platelets are dominated by interference effects between the light rays reflected at the different boundaries between the layers within the stacks (Land 1972).

In an earlier paper (Denton & Rowe 1994), the hypothesis was advanced that the reflecting structures in the external surfaces of silvery fish have properties that could allow such a fish to communicate information rapidly to its neighbours about its movements, as well as allowing the fish to conceal itself. This hypothesis was mainly supported by observations on the greater sand eel (*Hyperoplus lanceolatus*), whose silvery surfaces reflect light almost equally well across the whole of our visible spectrum.

Here, we consider fish in which some structures reflect strongly over only part of our spectrum, so that to us they appear as brightly coloured. The animal chosen for detailed study was the horse mackerel, *Trachurus trachurus*, for which Denton & Land (1971) have described the properties of some of its reflectors. They had the good fortune to be allowed to borrow from Sir Andrew Huxley the interference microscope which he had invented (Huxley 1954), and they used this instrument to measure the optical thicknesses (vt, where v is the refractive index and t is the physical thickness) of crystals from the reflecting platelets of a number of species of fish and squid. They showed that where the platelets are brightly coloured, their crystals usually have average optical thicknesses of a quarter of $\lambda_{\max}$, the wavelength at which they reflect best at near-normal incidence; typically optical thicknesses range from 120 to 157 nm giving a mean value for $4\,vt$ of about 550 nm, the expected value for an 'ideal' $\lambda/4$ stack of crystals and cytoplasmic spaces, reflecting in the green/yellow. The reflecting platelets of the dorsal flanks of the horse mackerel often appear to be blue, but become green when some associated black pigment is dissected away. Since the coloured platelets in *Trachurus* closely resemble those found under the scales of the herring in spectral reflectivity curves and in depth of colour, we believe that the platelets in *Trachurus* must also consist of a stack of about five crystals separated by cytoplasmic spaces (Denton 1970).

Most of the surface of the ventral flank of *Trachurus* has two, easily seen, superposed reflecting layers of platelets, which can be identified on histological preparations along with other reflecting layers internal to them both. The two layers together can be seen to be only about a few micrometres thick (see Franz 1907 and Denton & Nicol 1966, particularly their Plate VII D). By direct observation it proved easy to show that: (1) the external layer reflects red/orange light when white light falls on it at angles close to normal incidence to the surfaces of its platelets, and (2) the underlying layer reflects blue/green light in similar conditions.

Denton & Land (1971) found that crystals from a coloured area of a ventral flank had a wider range of optical thicknesses than those from the dorsal flank, the values for 4 *vt* extending from 450 to 780 nm. This is what one would expect if the skin in the ventral flanks contained two types of platelets, each of which consisted of close-to-ideal $\lambda/4$ crystal/cytoplasm stacks, with one layer's platelets reflecting in the green ($\lambda_{max} \sim 550$ nm) and the other in the red ($\lambda_{max} \sim 700$ nm), and each having the same variation in crystal thickness as in the more homogeneously coloured dorsal region.

(*b*) *The light environments within which the fish live*

The horse mackerel is a fish that makes considerable migrations from off-shore into coastal waters where it feeds largely on small fish such as herring fry. Sometimes it is found in immense shoals swimming close to the surface (Norman 1963, revised by Greenwood). Superposed coloured reflecting layers very like those described here in horse mackerel are found in mackerel, which is also a schooling fish, and Denton (1970) gives photographs of such layers. The mackerel migrates into the coastal waters from open oceanic waters and sometimes swims very close to the surface of the sea. Both species are, therefore, exposed during their lives to a wide range of lighting conditions. These include those found close to the surface which approximate in spectral composition and intensity to those found above the surface of the sea, and also those found away from the surface in oceanic and coastal waters where the light intensity is relatively low and confined to spectral bands centred around, for oceanic waters, blue light, and, for coastal waters, the green-yellow parts of our spectrum (see Tyler & Smith 1970; Jerlov 1976).

2. METHODS

(*a*) *Fish*

Experimental work was done on *Trachurus trachurus* and various other fish freshly killed by being placed in a suitable solution of the anaesthetic 2-methylbutan-2-ol (tertiary-amyl alcohol) until respiratory movements of the operculi and reflexes had ceased for several minutes.

(*b*) *Equipment*

Observations and measurements on reflecting structures were made using the following apparatus:

(1) A small tilting table, similar to that described by Denton & Nicol (1965) and shown on their text-figure 9. With this apparatus, observations were made using near-vertical illumination: (*a*) through a dissecting microscope (this method is only useful for small fish or for parts of fish), and (*b*) directly through a small aperture. For a given reflecting structure we found the angular settings of the tilting table which gave the brightest reflection and sometimes the range of angles of enhanced reflectivity around this maximum value.

(2) The apparatus described by Denton & Rowe (1994) for measuring the angular dispositions of reflecting platelets in the surfaces of fish. This apparatus is shown diagrammatically in their figure 12.

(3) An apparatus similar to that used by Denton & Rowe to simulate the distribution of light in the sea (see their figure 13), but improved by using a nearly cylindrical container made of white, light-diffusing plastic and an annular light source. In some experiments pieces of bright aluminium foil were laid against the surfaces of the fish so that, by finding the angles to which this foil reflected light, we could find the planes of the surfaces of the fish.

(4) The apparatus shown in figure 1 was used to measure spectral reflectivities. The specimen (**S**) to be studied was placed on a tilting table (**T**) and illuminated by a narrow beam of white light, which could be placed in several different positions varying from near-normal incidence (**LS1**) to an angle of incidence of about 45° (**LS2**). An image of part of its surface was formed by a dissecting microscope on a small slit or circular aperture (**A**) corresponding to an area of about one square millimetre on the fish. This led to a photo-multiplier (**PM**). The microscope only

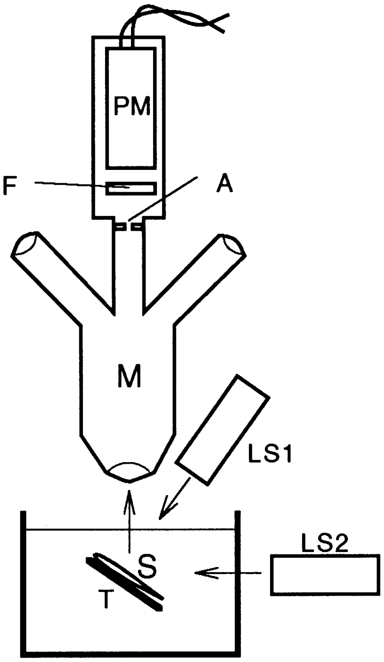


Figure 1. Apparatus used to measure spectral reflectivities. **S**, specimen on **T** tilting table; **M**, microscope; **A**, aperture; **F**, filter; **PM**, photo-multiplier; **LS1**, light source 1; **LS2**, light source 2.

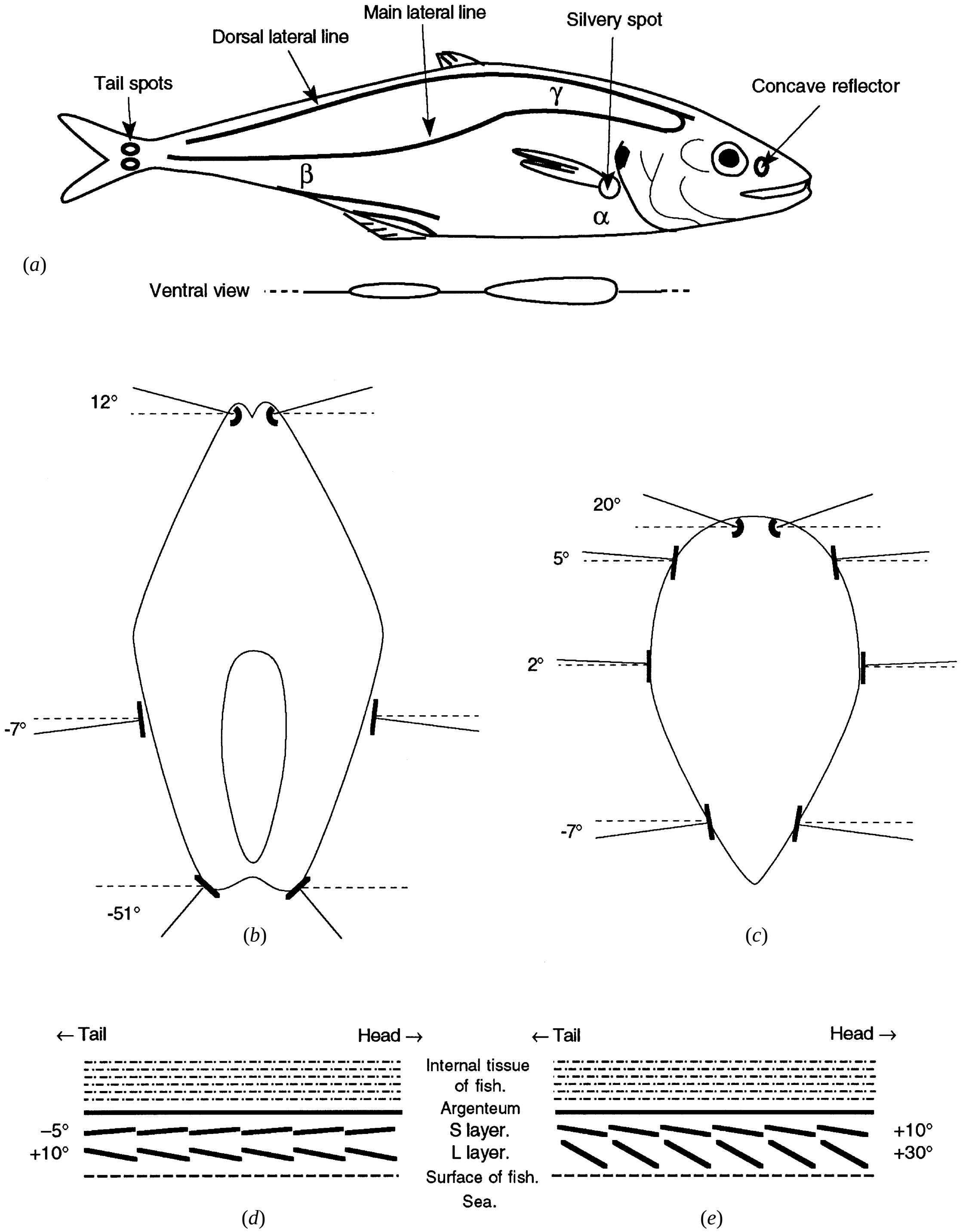


Figure 2. *Trachurus trachurus*. (*a*) Side view and ventral view of the fish indicating some of the structures and positions on the fish's surfaces referred to in the text. (*b*) Cross-section perpendicular to long axis of the fish in the region of the pelvic fin. It shows the orientations of some of the reflecting platelets; solid lines indicate the normal to platelets and dashed lines indicate the horizontal. The topmost orientations are for the dorsal lateral line. (*c*) Similar to (*b*), but for muscular tail region. (*d*) For area α of (*a*) part of horizontal section showing two superposed layers; the outer (here lower) layer is the **L** (red) layer, the inner layer (here upper) is the **S** (blue) layer. The platelets are in fact very small, typically about 20 μm × 5 μm. The short solid lines represent complete platelets, the individual crystals making up each platelet being too fine to be shown. (*e*) Similar to (*d*), but for the area β of (*a*).

accepted light over a range of angles of ±3.5°. Interference filters (**F**), which transmitted only narrow wavebands from the spectrum, could be interposed in the light beam to vary the waveband of the light reaching the photo-multiplier. The relative sensitivities of the system to the light transmitted by the various filters were found by measuring, for each filter, the output of the photo-multiplier to the light reflected by the surface of a freshly scraped block of magnesium carbonate. This surface is known to have almost constant reflectivity over the waveband used (Benford 1947).

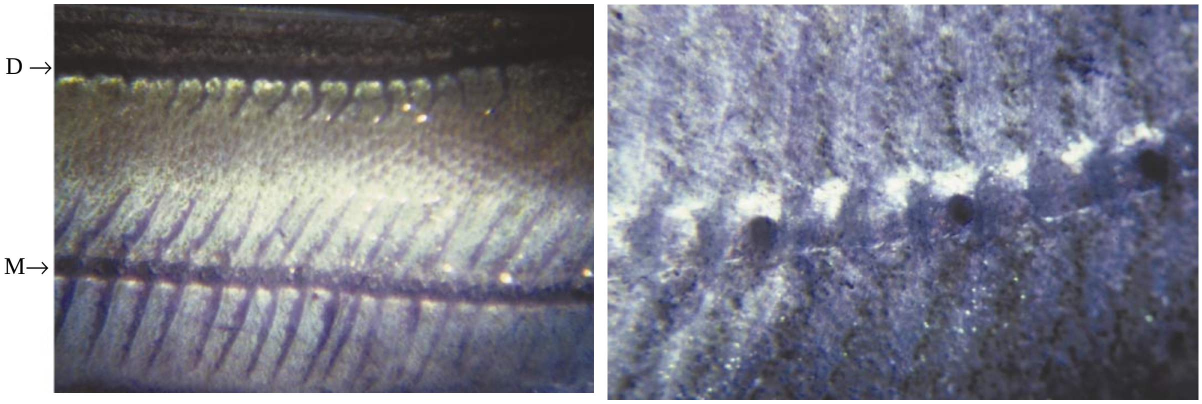


Figure 3. *Trachurus trachurus*. Photographs taken by A. C. G. Best and E. J. Denton of part of the body of a fresh fish. (*a*) The lateral-line canals (shown by arrows) filled with a solution of Janus green B. D corresponds to dorsal lateral-line canal, M corresponds to main lateral-line canal. (*b*) The dye shown in (*a*) has been washed out and the heavily stained neuromasts can readily be seen in the main canal. There are no neuromasts in the dorsal canal.

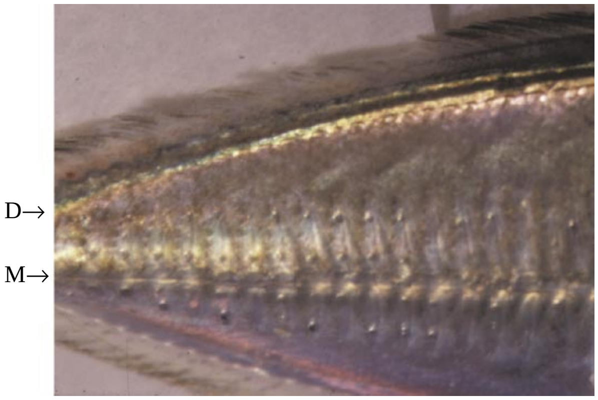


Figure 4. *Trachurus trachurus*. Fresh fish illuminated by an approximately parallel beam of light. The dorsal lateral-line canal has reflecting platelets orientated so as to reflect light in a more upwards and more tail-wards direction than those of the main lateral-line canal and, more upwards, but almost equally tail-wards, than those of the **L** (red) reflecting layer on the fish's ventral flanks.

(*c*) *Symbols*

In this paper, the symbols have the same meanings as in Denton & Rowe 1994 (see their figures 7 and 8). Thetas are used for angles in planes perpendicular to the long axis of the fish, (angles in the plane of roll) and epsilons for angles in horizontal planes perpendicular to that containing the mid-dorsal and mid-ventral lines (angles in the plane of yaw). Since the reflecting platelets are generally not parallel to the surface in which they lie, it is necessary to describe the two orientations separately. θ_p and ϵ_p are the appropriate angles between the surface of a platelet and the vertical, mid-line plane of the fish. θ_t and ϵ_t are the appropriate angles between the tangents to the surface of the fish and its mid-line plane. θ and ϵ define the orientation of a platelet with respect to the surface in which it lies. Therefore $\theta = \theta_p - \theta_t$ and $\epsilon = \epsilon_p - \epsilon_t$.

In the discussion which follows, σ is used for the angle between the normal to the surface of a fish at a point and a line from that point to another point from which a fish is being observed. When the point of observation is in a horizontal plane containing the fish, σ is positive for points of observation towards the tail of the fish and negative for points towards the snout. κ is used for a similar angle, but relative to the normal to a reflecting platelet, so if a platelet is set at an angle ϵ relative to the surface then $\kappa = \sigma - \epsilon$.

3. RESULTS

(*a*) *Observations on some of the reflecting structures in the surfaces of* Trachurus trachurus

Figure 2*a* shows where the observations and measurements were made on the fish.

(i) *The tail and the pectoral fins*

On each side of the base of its tail, *Trachurus* has two brightly reflecting patches; when illuminated by white light, one patch appears reddish and the other yellowish. The platelets of these patches have their surfaces inclined about five degrees downwards and about four degrees tailwards. The pectoral fins of this fish are used as the sole method of propulsion during manoeuvring, swimming slowly and hovering. Each pectoral fin has a very silvery patch at its base. This is turned towards and away from the surface of the sea whenever the fin is used. When viewed from above in a sea water tank with overhead lighting such patches can sometimes be seen to give a series of bright flashes of light when the fish is 'sculling'.

(ii) *The dorsal lateral-line canal*

Trachurus has both a dorsal and a main lateral-line canal on each side of its body. The dorsal lateral-line canal is a tube within the skin. It runs almost the whole length of the body lying quite close to the mid-dorsal line. This canal is connected by short side-tubes to the external medium (figure 3*a*).

Mr A. C. G. Best and one of us (E. J. D.) have made a detailed anatomical and histological study of the lateral-line system of *Trachurus trachurus*. No sign of neuromasts, or indeed any sensory structures associated with the body's dorsal lateral line could be found. In contrast, the neuromasts of the main body and head lateral lines could readily be seen either by staining fresh material with vital stains such as Janus Green B

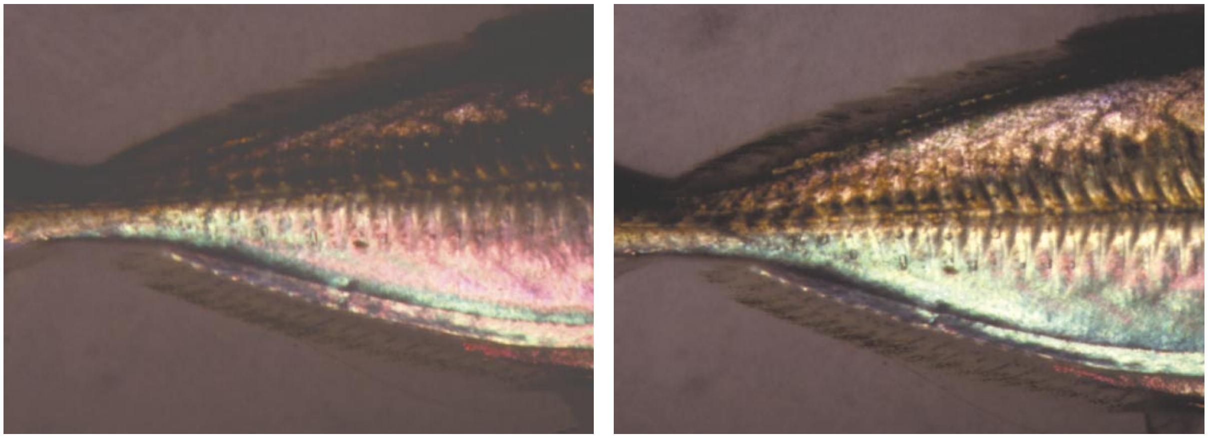


Figure 5. *Trachurus trachurus*. (*a*) and (*b*) are photographs of the same fish illuminated by a source of white light. The direction of the incident light has been made such that the light reflected to the camera comes, in (*a*) from the outer **L** (red) layer of reflecting platelets and in (*b*) from the inner **S** (blue-green) layer of platelets.

Figure 6. *Trachurus trachurus*. A photograph of the head of a fish illuminated by an approximately parallel beam of light. The mirror in front of the eye and the differences in colour and brightness between the various surfaces of the head can be seen. Some of the patches on the head which appear coloured in life, appear white in the photograph due to unavoidable overexposure.

(figure 3*b*) or on stained serial sections of fixed material. The inner walls of the dorsal canal have a high reflectivity, whilst the outer walls are transparent so that the canal to some degree resembles a long cylindrical, outwardly-facing, mirror (figure 4). However, the reflective patterns which it gives are complicated by reflections from the side tubes and neighbouring silvery tissues and by pigmented cells in the skin that restrict the directions in which light can enter or escape. On three fish (of lengths 3.5, 10 and 25 cm) the angles θ_p and ϵ_p (between reflecting surface of the canal and the axis of the fish) were found for dorsal and main lateral-line canals in the region marked γ on figure 2*a*; for the dorsal canal, the reflecting structures were orientated to face upwards and tailwards, the values for θ_p being 12°, 20° and 28° (upwards) (e.g. figure 2*b*), whilst the values for ϵ_p were 24°, 18° and 20° (tailwards). These values show that the dorsal lateral-line canal behaves as a reflecting surface whose reflecting units, the platelets, are turned towards the tail of the fish as well as sideways and upwards. The upward angular limit to the reflection of light by the dorsal lateral-line canal is determined by dark pigment above this canal. In a fresh preparation this upper limit is sharp, being at about 50° from the horizontal.

Figure 4 shows that the dorsal lateral-line canal has very different properties from the dorsal flank in which it lies. When illuminated with white light, the reflected light from the canal is bright yellow, whilst the dorsal flank appears blue. The orientations of its reflecting platelets are also very different; those of the dorsal flank being inclined only a few degrees from being vertical and tipped through a much smaller angle tailwards.

The dorsal lateral line certainly acts as a light reflecting organ, but it may well have other functions; Dr Daniel Weihs has suggested that it may well be useful hydrodynamically (personal communication).

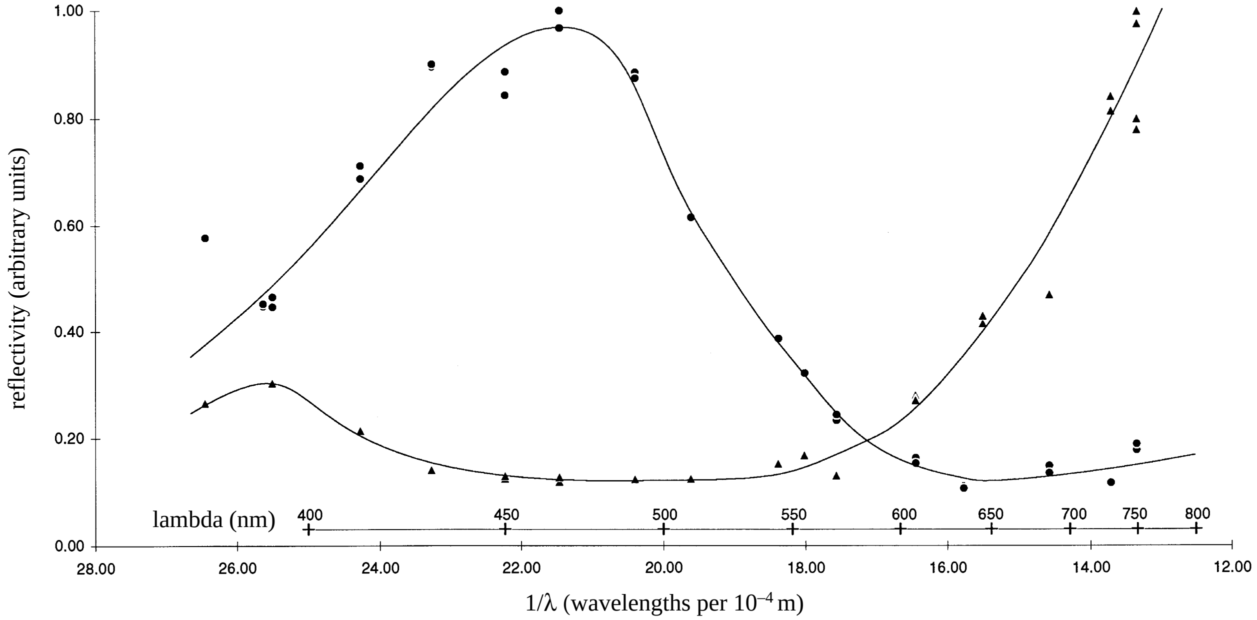


Figure 7. Spectral reflectivities for the S and L layers of a specimen of *Trachurus trachurus* of approximately length 7.5 cm. Measurements made in region α of figure 2 (*a*), for an angle of incidence of 15° to the platelets. ● signifies data points for the S layer; ▲ signifies data points for the L layer.

(iii) *The main lateral-lines*

Each main lateral line is formed by the juxtapositioning of openings in one line of very large specialized scales (the scutes) so that they form a canal along the body of the fish. Sea water can pass into and out of this canal through channels in these scales. The main canals have slightly different reflective properties from the surrounding surfaces of the fish, but their reflectors are much closer to being parallel to the surfaces on which they lie than are those of the dorsal canal.

(iv) *The ventral flanks of body*

The most conspicuous feature of the ventral flanks is that, when illuminated with narrow beams of light, their colours change greatly with the angle of view; in this they are like corresponding regions of the surface of the mackerel (*Scomber scombrus*). When illuminated with a beam of white light at moderate (less than about 30°) angles of incidence, then they appear predominately red when the observer is to the side and tailwards of the fish, and blue/green when viewed from the side and ahead of the fish (figure 5). The colours differed little between different specimens but there were appreciable differences between different areas. For example, there was an area α beneath the pectoral fin (see figure 2*a*) for which, using a white tungsten source, the blue colour was without any suggestion of green and the red was purer than that for other parts of the ventral flanks. As we have noted above, these coloured reflections come from two conspicuous superposed layers of reflecting platelets in the skin, one layer reflecting mainly the longer wavelengths of our visual spectrum and the other the shorter wavelengths. We shall refer to these layers as the L (for long wavelength) and S (for short wavelength) layers, respectively.

Orientations of the platelets in these two layers were found for different parts of the ventral flanks on several fish (e.g. figure 2*b*, *c*). For the main part of the ventral flank, the values of θ_{p} were in general around $-7°$ in a dorso-ventral direction (i.e. the platelets faced slightly downwards) and the difference in angles ϵ_{p} that gave the strongest reflections for the S and L layers were around 15° (range 13° to 21° for four measurements). The S platelets were inclined around $-5°$ (i.e. towards the head) and the L platelets by around 10° towards the tail (see figure 2*d*). Neither the L nor the S layers were completely specular but almost all the light reflected by such a layer was usually contained in a range of angles of between plus and minus 5° from the angle for which the reflection was brightest. For the area β of figure 2*a* the differences between the values of ϵ_{p} that gave the strongest reflections for the S and L layers were around 16° (range 14° to 18° with five measurements); the L reflecting platelets were inclined more towards the tail than the S reflecting platelets. The absolute values of ϵ_{p} for which the brightest red reflections were given were around 24° (range 17° to 28°), and for the blue around 8° (range 3° to 10°) (see figure 2*e*).

Internal to the S and L layers is an argenteum, which reflects less specularly than the outer layers. Its reflecting surfaces are approximately parallel with the surfaces under which they lie, so that they reflect light from directions for which the radiances are less than those for the S and L layers.

(v) *The head*

The variety of the reflecting structures over the surfaces of the head of *Trachurus* are just as great as over the body. There are some areas, especially behind and below the eye, for which the colour reflected varies greatly with the angle of viewing and the direction of the incident light (as with the flanks); however, such

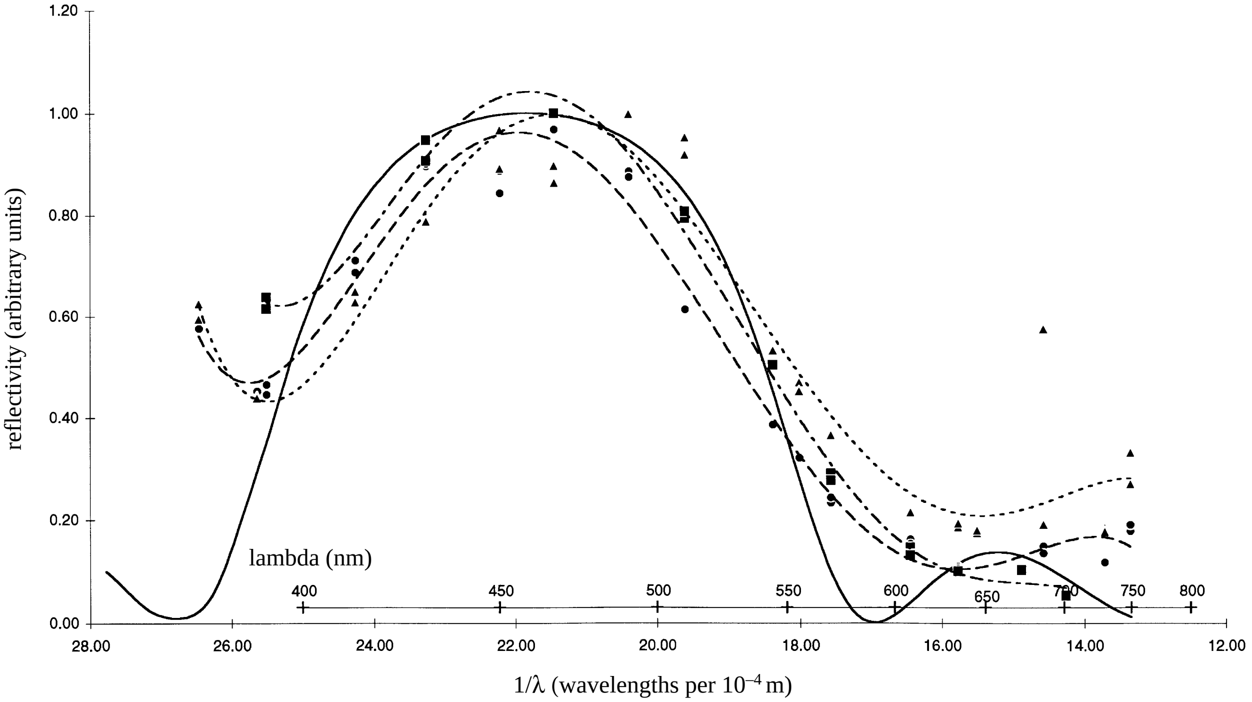


Figure 8. Experimental data for the **S** layer of figure 7 (data points: ●, lines: – – –), together with similar data for the same preparation two hours later (data points: ▲, lines: -----), and for another specimen kept in cold sea water for two days after death (data points: ■, lines: – -·- -). The solid curve (shown: ——) is based on a calculation for an ideal $\lambda/4$ stack of 5 crystals at an angle of incidence of 15° and having $\lambda_{\max}$ of 470 nm at normal incidence.

areas show great local variation in the orientations of their reflecting platelets and in their spectral reflectivities. As before, these colour changes are caused by superposed layers of platelets differing in spectral reflectivities and orientations; these platelets are mostly inclined towards the snout, the **L** reflectors being more inclined than the **S** reflectors.

A reflecting structure, which has no parallel on the body, is found immediately in front of each eye. This has the appearance of a large concave mirror and can be clearly seen on the photograph of figure 6. This reflecting surface is on the lower surface of a large canal; the upper surface, separating the canal from the surrounding sea, is reflective near the snout but becomes transparent in front of the eye. These areas, as well as the outer surfaces of both the upper and lower jaws, appear highly reflecting at all visible wavelengths.

(vi) *The ventral surfaces*

On either side of the mid ventral line, along the outer edges of the ventral surface where it meets the ventral flanks, there is a narrow band of reflecting platelets (figure 2*a*) whose surfaces are directed downwards and backwards towards the tail; measured values for two fish were, for θ_p: 51° and 47° and for ϵ_p: 22° and 18°.

(*b*) *Measurements of spectral reflectivities*

Some spectral reflectivities were measured with the apparatus shown in figure 1 and compared with reflectivities calculated from equations given by Huxley (1968) for the reflection of light by multi-layer structures thin enough to show optical interference; these equations have also been used by Land (1972) who applied them to a variety of reflective structures found in animals.

Figure 7 shows the measured spectral reflectivities of the **S** and **L** layers of a specimen, of length approximately 7.5 cm, for the area α of figure 2*a*. For each layer, the specimen was manually oriented to achieve maximum specular reflection with an angle of incidence of 15° to the platelets of that layer. Since the platelets of the **S** and **L** layers are set at different angles with respect to the surface of the fish, it is possible to measure the spectral reflectivity of the two layers independently. It can be seen that the reflectivity of the **S** layer reaches a maximum at about $\lambda = 460$ nm; the position of the maximum for the **L** layer is less easy to estimate since the photo-multiplier is relatively insensitive to these wavelengths, but other measurements suggest that it is close to 730 nm.

Figure 8 compares the reflectivities of the **S** layer shown in figure 7 with those found two hours later for the same preparation, and those found for another preparation from a fish which had been two days in cold sea water after death. This shows that the preparation deteriorates very slowly. The experimental data (dotted curves) are compared with that predicted by Huxley's equation (solid curve) for an ideal $\lambda/4$ stack of five crystals, with $\lambda_{\max}$ of 470 nm (at normal incidence). The reflectivities of the platelets were measured at an angle of incidence of 15°, and the same value was used in the predictions; this would have caused a slight shift in $\lambda_{\max}$ of all curves towards the blue (see § 4*d*(ii) for further discussion). The agreement between the experimental data and prediction is good.

Figure 9 shows the spectral reflectivity of the **L** layer

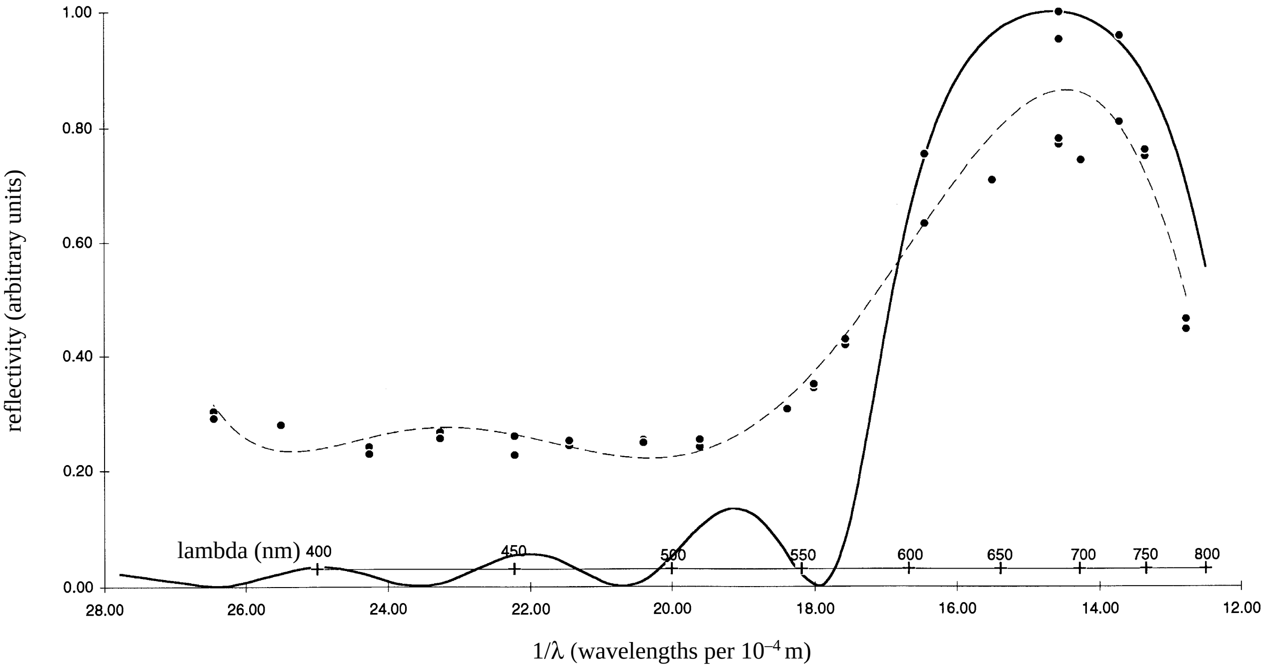


Figure 9. Spectral reflectivity of the **L** layer of a specimen, of length approximately 19 cm, for the area α of figure 2*a*. (data points: ●, lines: – – –). The solid curve (shown: ——) is based on a calculation for an ideal $\lambda/4$ stack of five crystals at an angle of incidence of 15° and having λ_{max} of 700 nm at normal incidence.

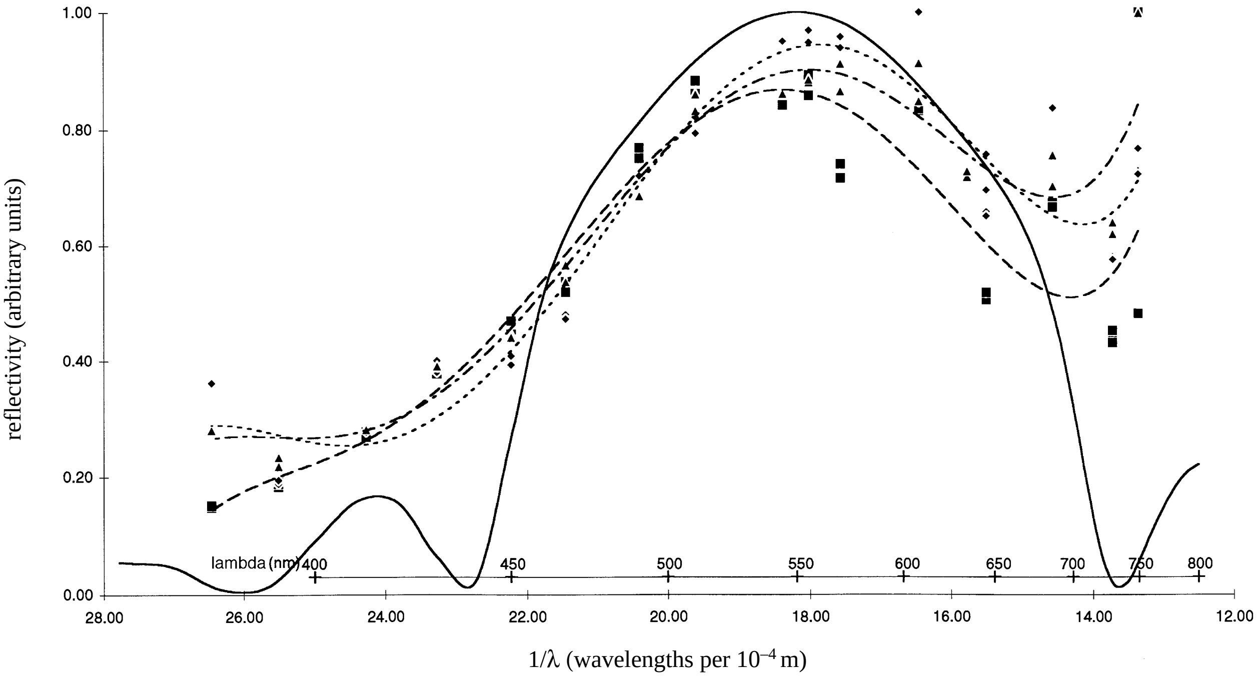


Figure 10. Spectral reflectivity of the same layer as for figure 9, but for an angle of incidence of 45°. The dashed curves are for three sets of measurements and the solid curve is based on a calculation for an ideal $\lambda/4$ stack of five crystals which would have λ_{max} of 700 nm at normal incidence, but which has an angle of incidence of 45° here.

of a larger specimen, of length approximately 19 cm, for the area α of figure 2*a*. The solid curve is based on calculation for an ideal $\lambda/4$ stack of five crystals with λ_{max} of 700 nm (at normal incidence). The reflectivity of the **S** layer (not shown) shows good agreement with the theoretical curve for an ideal $\lambda/4$ stack of five crystals with λ_{max} of 535 nm at normal incidence.

Figure 10 is also for the **L** layer of the same specimen, but here the measurements were made at an angle of incidence of 45°. Three sets of experimental data are shown, together with a curve based on calculations for an ideal $\lambda/4$ stack of five crystals with $\lambda_{max} = 700$ nm at normal incidence. For an angle of incidence of 45°, λ_{max} of the theoretical curve has shifted to about 550 nm, which gives a reasonable agreement with the measured curve.

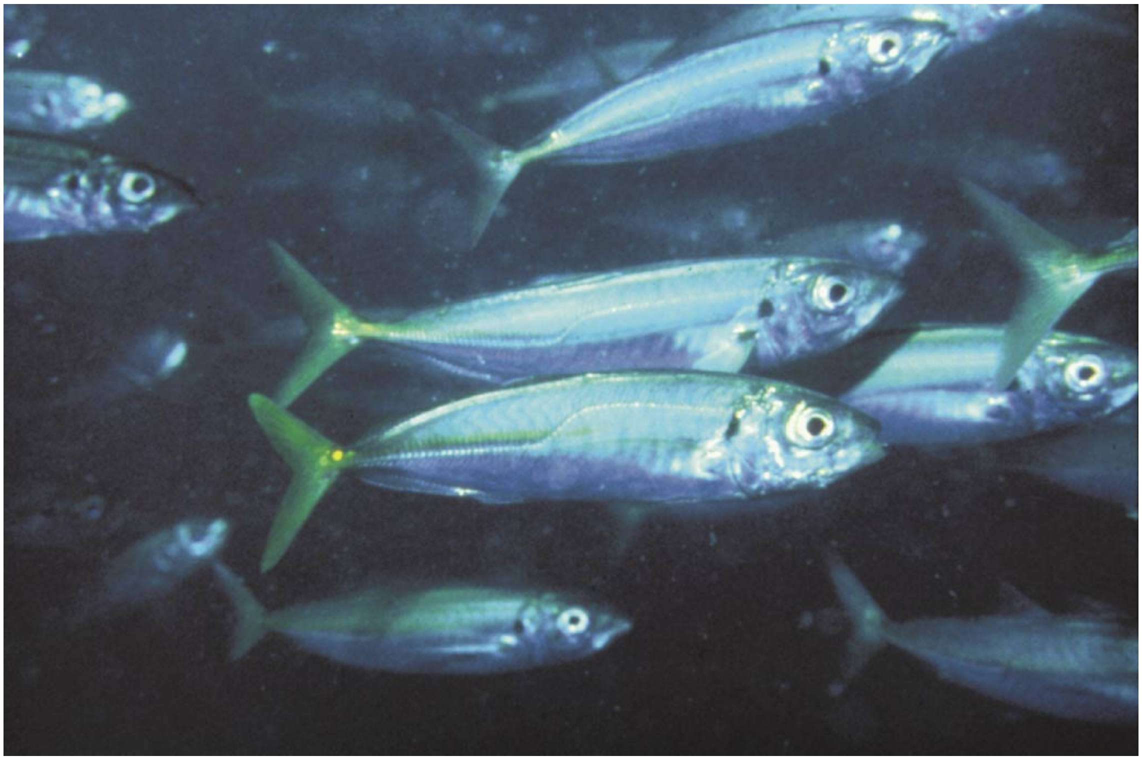


Figure 11. Photograph, taken by Dr M. P. Francis of *Trachurus novazelandiae* (the jack mackerel or yellowtail) in the sea by flash from the side of the fish. The brightly coloured yellow tail spots are very visible on some fish as are the lateral lines.

(*c*) *Effects of polarization*

Some observations were made on the ways in which reflectivities of some of the silvery layers of the greater sand eel and the horse mackerel were affected by polarization.

A sand eel was examined in the apparatus made to simulate natural light in the sea by an observer who rotated a polarizing filter in front of his eye. The effects of polarization were small when the fish was viewed obliquely from either the tail-end or the head-end. There was however a marked change in appearance with polarization when it was viewed from the side. This change was most marked for a band along the flank in the region between the D and T bands (shown by Denton & Rowe (1994) in their figure 14). When the long axis of the fish, i.e. head to tail, and the plane of polarization were horizontal, the D/T band was dark. When the plane of polarization was vertical the D/T band was bright and appreciably bluer. When the fish was rotated around a horizontal axis perpendicular to the length of the fish (so simulating changes in pitch) the polarization effects remained unaltered when referred to the long axis of the fish.

When horse mackerel were observed with directional lights at oblique angles of incidence using the light source LS2 with the apparatus shown in figure 1, marked polarization effects were seen. The highest ratio of the intensities of light polarized horizontally to light polarized vertically were seen at around the Brewster angle. (This is the angle at which the refracted and reflected rays at a single interface are 90° apart and the reflected ray is plane polarized.) However the above ratio was never less than 0.5. In part at least, this can be explained by the fact that the platelets in a given surface are not exactly parallel to each other and the microscope accepted light over a range of angles of $\pm 3.5°$. However, when fish were viewed in the apparatus simulating natural light, no striking changes in brightness were given by rotating a polarizing filter before the eye.

(*d*) *Possible osmotic effects*

If a live or freshly killed herring is placed successively in waters of different salinities, e.g. sea water and 1/2 sea water (one part of sea water to one part of water), the colours of the posterior parts of the scales change colour (Denton & Saunders 1972). This is because the spaces between the crystals of guanine change as the cells, within which the reflecting platelets lie, swell or shrink as they take up or lose water osmotically (Bone & Denton 1971). The anterior parts of the scales do not change colour because an osmotic barrier in the skin ensures that these parts are not subject to osmotic changes in the medium. It did not seem likely that the coloured reflecting layers studied in the present experiments on *Trachurus* would be as sensitive to the osmotic strength of the external medium as the posterior parts of the scales of the herring since the coloured reflecting layers in *Trachurus* lie beneath the dermis. But since our specimens were dead, it seemed best to look for changes in colour with osmotic changes in the medium. To this end, the colours of the L and S layers on the ventral flanks of a specimen of *Trachurus* were observed during a number of changes of the bathing solution between full strength sea water and sea water diluted to a half and to one third with fresh water. No changes in colour were observed.

4. DISCUSSION

(*a*) *Comparison with the greater sand eel*

Although the reflecting layers in the external surfaces of the greater sand eel and the horse mackerel appear at first sight to be very different, in many respects they are similar in the type of potential information that is displayed to neighbours in a school.

Rolling movements in both species are signalled by the whole side of the fish becoming generally brighter or darker than the background of natural submarine light against which it is viewed (the side viewed appearing brighter if it is turned to face in a more upwards direction).

Yawing movements in both species are signalled by differences in brightness between special areas in which the surfaces of the platelets are not parallel to the body surfaces in which they lie, but are tipped either towards the tail or towards the snout. The brightness of such surfaces depends on the angles at which its platelets are viewed, since the inclinations of the reflecting platelets on the surfaces in which they lie produces 'Venetian blind' effects whereby the observer from some angles of viewing sees the reflections from the platelets, but from other angles of viewing sees between the platelets to the underlying layers (see the Appendix, and also figures 9, 10 and 11 of Denton & Rowe (1994)).

Pitching movements were shown by Denton & Rowe to be signalled by areas on the surfaces of the signalling fish in which the platelets are tipped either rostrally or caudally with respect to the surface within which they lie. When the fish makes pitching movements, these areas of the fish's surface become either brighter or darker than other areas in which the platelets are parallel to the surfaces in which they lie.

However, there are marked differences between the reflecting layers of the greater sand eel and the horse mackerel, with the latter possessing more specialized reflecting structures and making far greater use of colour. The following discussion considers how these factors may be used for enhanced communication between neighbours in a school.

In the horse mackerel, but not significantly in the sand eel, there are areas of platelets which approximate to ideal $\lambda/4$ stacks of crystals of guanine and cytoplasm, and so have a band of high spectral reflectivity which moves progressively to the shorter wavelength end of the spectrum as the obliquity of the angle of viewing increases from the normal to the surface of the platelet (see figure 10). Consequently, a surface with one layer of such platelets could be used to signal changes in the angle of yaw by changes in colour. Some areas on the dorsal flanks of the horse mackerel seem to have such a single layer, but other areas have superposed layers differing in both spectral reflectivity and orientation.

We therefore give below an account of the kinds of changes in reflectivity expected of such an arrangement of platelets with rolling, yawing, and pitching movements. Thus for example, when this fish dives, we should expect the **L** layer on the ventral flank to become brighter than the **S** layer because platelets of the **L** layer are tipped about 20° more towards the tail and so will reflect light originating from a more upwards direction. We may note that if the waveband being seen is one for which the sea absorbs light relatively heavily, the change in radiance with angle in the vertical plane will be greater than for wavebands to which the sea is more transparent (Duntley 1963; Timofeeva 1974). For the more heavily absorbed lights, the effects of rolling and pitching will therefore be greater.

(*b*) *Some specialized reflecting structures*

(i) *Tail and pectoral fins*

The silvery patches on the tail and at the bases of the pectoral fins must give very direct and early information on the fish's activities. Such reflecting patches are common features of silvery fish (figure 11). In a previous paper, Denton & Rowe (1994), we have argued that tail reflectors can give very powerful stimuli to the eyes of neighbours, but that, because they are small sources, they will give only weak signals to distant observers.

(ii) *The lateral lines and the 'mirror in front of the eye'*

The orientations of the reflectors in the dorsal lateral line are such that when the fish is swimming in a horizontal plane in the sea, the dorsal lateral line will be brighter than the background light fields to observers above and behind the fish, whilst being dark to observers in a large part of the field from which it can be viewed from behind and below the fish. This could evidently be a useful guide to fish manoeuvring to hold station in a school of fish. The dorsal lateral line of a horse mackerel will appear to a neighbouring fish, positioned either alongside or behind it, as a thin bright line indicating the direction in which the observed fish is pointing. The apparent length of this line will shorten if the 'receiving' fish begins to pass the observed fish. In contrast, if the fish turns to swim upwards the line will become less bright. Sideways motions of the line will signal propulsive movements in a similar way to the tail patches mentioned above, but will be visible from different directions.

Analogous information on a fish's movements will be given to neighbours ahead and above of it by changes in the pattern of light reflected by special reflecting structures on the head. The 'mirror in front of each eye' reflects strongly only in a direction forwards and slightly upwards and outwards relative to the fish. This reflecting surface is fixed relative to the skull of the fish, whereas other nearby reflecting surfaces move with the upper or lower jaws, or with the operculum.

(*c*) *The spectral band useful for vision for* **Trachurus**

Anyone who has caught a mackerel on a sunny day must have been impressed by the display of iridescent colours that accompany its movements. These range over the whole of our visual spectrum, from deep blue to red. If reflections of light are important in passing information on movements between neighbouring fish, it seems very probable that such wide changes in colour play a significant role.

There are, however, good reasons for believing that the spectral band useful for vision in these fish is generally less wide than in man. Thorpe *et al.* (1993) have examined lenses from the eyes of 23 specimens of *Trachurus trachurus*, covering a wide range of sizes. These lenses, which covered a range of diameters of between 1.72 and 5.42 mm, all contained stable pigments in sufficiently high concentrations to prevent any significant light of wavelengths less than 400 nm reaching the retina, and we shall take this wavelength as being the lower limit of the spectral sensitivity of this fish. The spectral absorption of the lenses of the mackerel (*Scomber scomber*) varies with the animal's age. The younger animals have lenses which are transparent to wavelengths down to about 360 nm, whilst the lenses of older animals cut off light of wavelengths below about 400 nm (Thorpe & Douglas 1993).

Other limits to the spectral band available for vision in fish depend on the type of seawater and the depth in that seawater at which they are living.

Let us recall the spectral properties of the light found in the seas within which the fish used in our experiments live. These differ from one another in the rates at which lights of different wavelengths diminish with depth. For oceanic waters we may take the measurements of Tyler & Smith (1970) as examples. In one series of measurements on the Gulf Stream, they found that at 25 m depth, the downward irradiance for $\lambda = 480$ nm was about 1/2 of its value at the surface, but for $\lambda =$ 550 nm the corresponding factor was about 1/10, for $\lambda = 600$ nm it was about 1/300 and (red) lights of $\lambda >$ 600 nm were even more rapidly attenuated. If this differential attenuation continued at greater depths, the light of $\lambda = 550$ nm would soon become unimportant for vision. This does not, however, seem to be the case. From the measurements of Kampa (1970), who worked on oceanic waters at greater depths but over a more restricted range of wavelengths, we find that at 150 m depth the irradiance of light of $\lambda =$ 533 nm had diminished below that found at the surface about ten times more than had blue lights of around $\lambda = 470$ nm, which are the ones to which the sea was most transparent. Below 150 m (at least down to 500 m), lights in the waveband 400–550 nm all fell in the same way; for example, the ratio of the irradiances at $\lambda = 470$ nm and at $\lambda = 550$ nm stayed at about 1:10. On the basis of results of this kind, we shall assume that, for fish like the horse mackerel and the mackerel in oceanic waters, it is the range of wavelengths between 360 and 600 nm for which colour discrimination is likely to be most generally helpful. However, when such fish come close to the surface their light environment approximates more closely to our own.

In coastal waters, it is green rather than blue light which in best transmitted. In the English Channel a few miles from Plymouth, at a time of year when thermocline would have been established, Atkins (1945) found that within the waveband blue to yellow, there were appreciable differences in the absorption of light at different wavelengths in the first 20 m, but below that depth the differences in absorbtion were very small. In the English Channel, as in similar coastal waters, the intensity of light begins to fall rapidly with increasing depth for light of wavelength > 600 nm; thus we take 620 nm as a common upper limit to the waveband which is available for vision.

We have no specific information on the spectral sensitivities of the photosensitive pigments in the retinae of *Trachurus* and *Scomber*. However, Partridge (1990), in his excellent review, notes that many fish have evolved colour vision, with marine species being most sensitive in the blue and in the green parts of the spectrum. So whilst recognizing that *Trachurus* and *Scomber* might have retinal photosensitive pigments absorbing maximally at longer or shorter wavelengths, it seems probable that they have receptors absorbing maximally in the blue/green wavelengths.

(*d*) *The reflectivity of single and of superposed reflecting layers*

(i) *Questions to be resolved*

With regard to the coloured reflecting surfaces of *Trachurus*, three questions present themselves:

(a) What are the advantages of having coloured reflectors?

(b) What is the point of reflecting red light, as some layers do, when there is virtually no red light to reflect under the sea?

(c) What advantage can there be in having *two* reflecting layers set at different angles and reflecting different wavebands?

Agreement between the experimental results described above and the theoretical predictions of Huxley (1968) applied to $\lambda/4$ stacks of five crystals and cytoplasmic spaces are sufficiently good to encourage us to discuss these questions in terms of such stacks. A number of computations were carried out using Huxley's equations to determine the influence of various parameters.

(ii) *Single layers of platelets*

We consider first the simple case of a surface containing a single layer of platelets in which the platelets are all vertical (or inclined at the same angle with respect to the vertical) in a light field which is symmetrical with respect to the vertical (see figure 12*a*). The platelets are assumed to be five-layer stacks of guanine (refractive index = 1.83) separated by cytoplasm (refractive index = 1.33) (Land 1972). Each stack is 'ideal' in the sense that the optical thickness of each layer and each separating space is the same.

Figure 13*a* shows the spectral reflectivity given by Huxley's equations for such a stack with $\lambda_{\max} =$ 730 nm (at normal incidence), illuminated by light polarized normal to the plane containing both incident and reflected rays, and figure 13*b* is for light polarized parallel to this plane. At each point within the chart

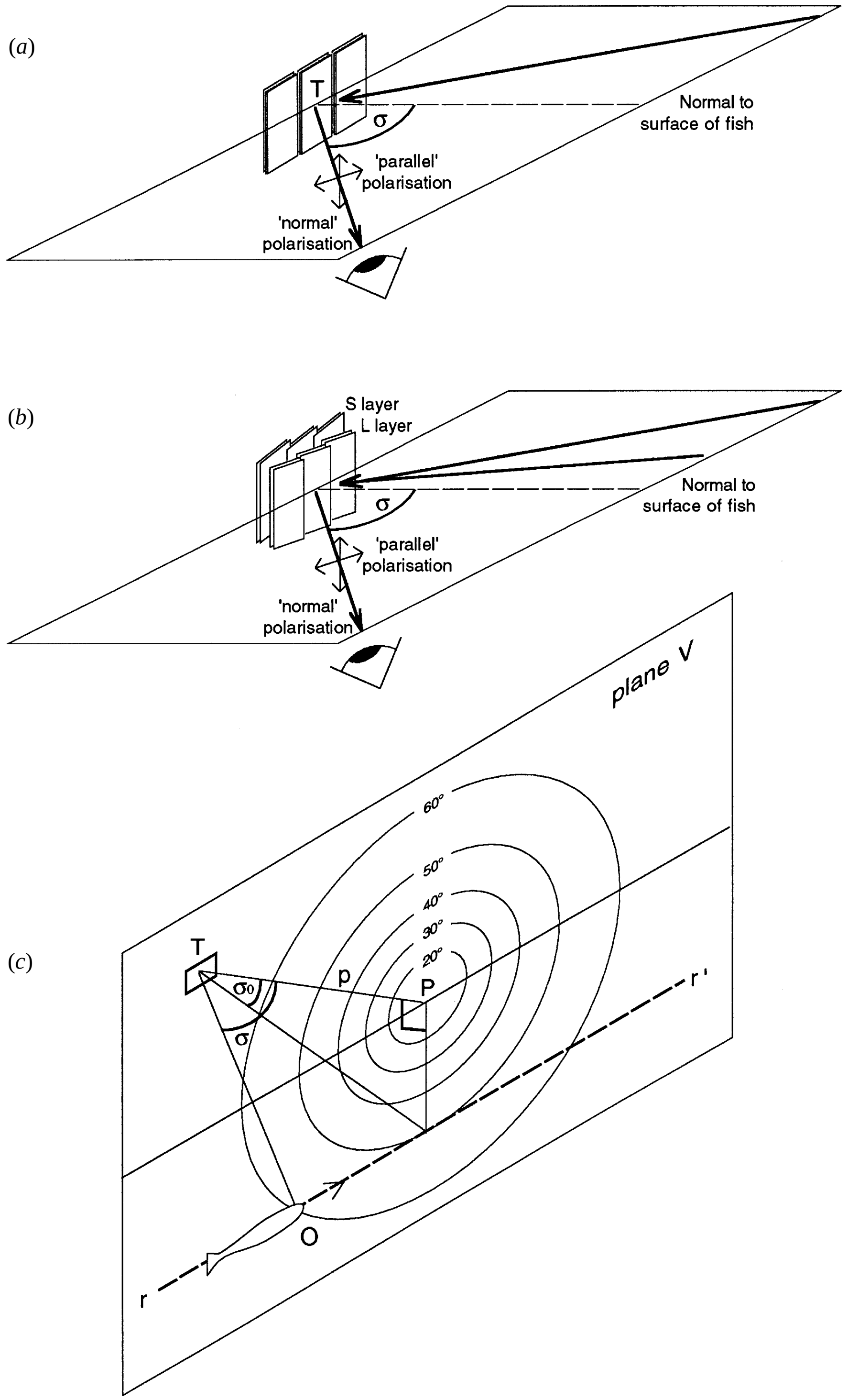
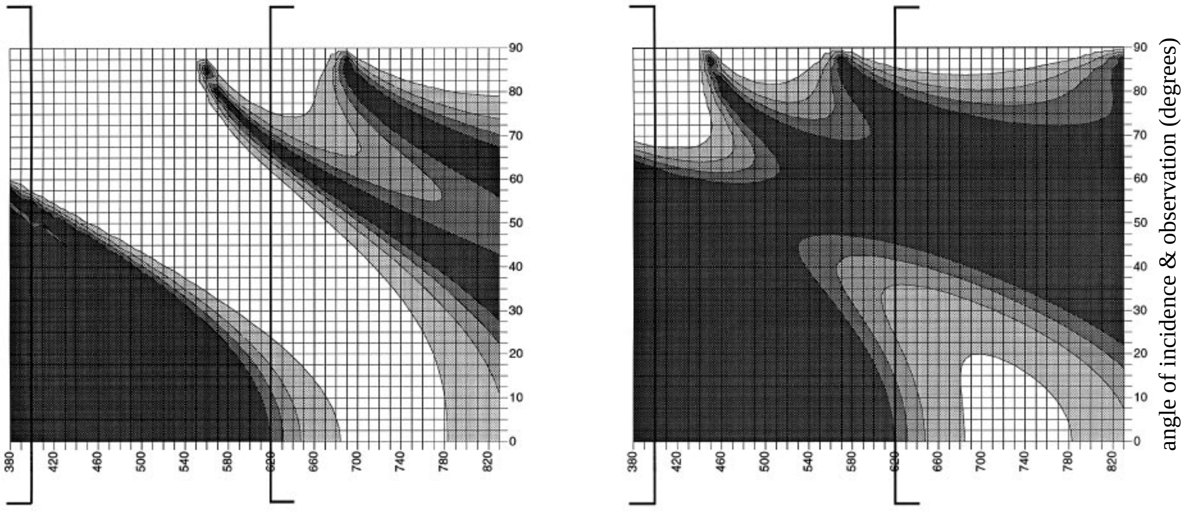


Figure 12. Diagrams illustrating (*a*) the configuration for which figure 13 was computed; (*b*) the configuration for which figure 14 was computed; (*c*) the relations between the angles (σ) subtended by an observing fish O on a reflecting surface T for various positions along horizontal lines in a vertical surface, V, which is parallel to the surface T. TP is a perpendicular from T on to V.

area, reflectivity is shown by the shading, with light or no shading indicating high reflectivity and heavy shading indicating low reflectivity. Each figure shows how the reflectivity varies with the wavelength of the incident light and with the angle of incidence. With such interference effects, any light not reflected is transmitted and in these calculations it is assumed that all transmitted light is lost. In the fish, transmitted light would be largely absorbed in tissues underlying the platelets, or scattered. Negative angles of incidence (0° to −90°) are not shown, since the physical arrangement is symmetric around the normal, and so the extension of the chart for negative angles would simply be the mirror image (about the 0° axis) of the chart shown for positive angles.

It can be seen that at normal incidence (0°), and for (*a*) polarization normal to plane of ray. λ$_{max}$: 730 nm. (*b*) polarization parallel to plane of ray. λ$_{max}$: 730 nm.



(*c*) polarization normal to plane of ray. λ$_{max}$: 470 nm. (*d*) polarization parallel to plane of ray. λ$_{max}$: 470 nm.

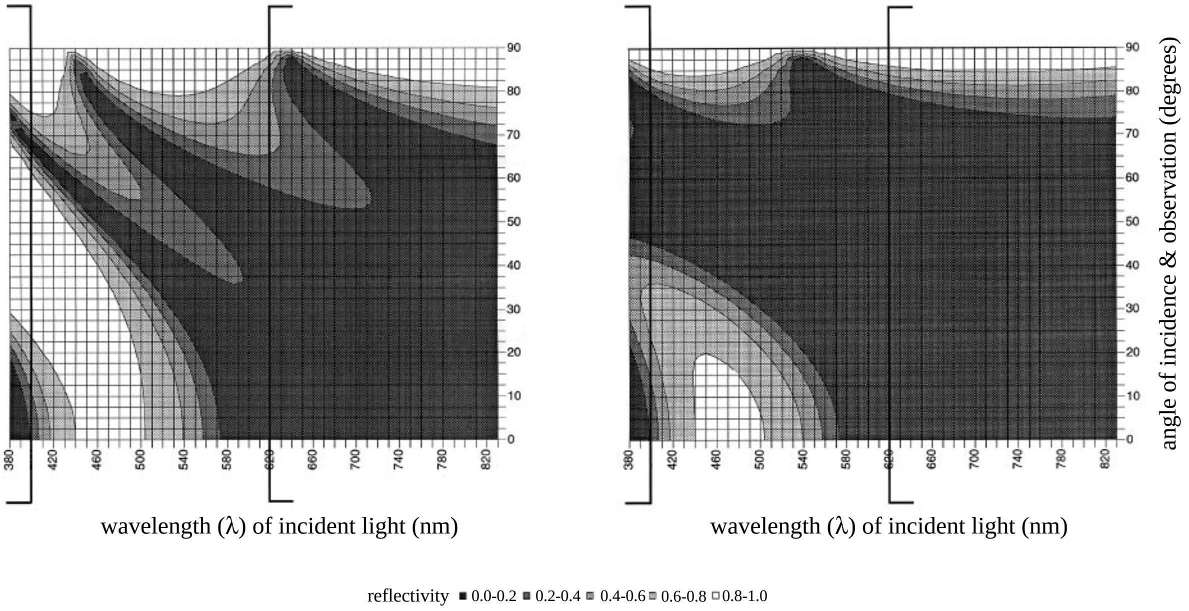


Figure 13. Calculated spectral reflectivities for a single layer of platelets at various wavelengths λ and at various angles of observation σ. All the platelets are assumed to have their surfaces parallel to the surface in which they lie (i.e. θ: 0°, ϵ: 0°) and to be ideal $\lambda/4$ stacks. The degree of shading at each point represents the reflectivity, such that light shading represents high reflectivity (and hence low transmission) and vice versa for dark shading: (*a*) λ_{max} of platelets: 730 nm. For light polarized normal to the plane of the ray, (*b*) λ_{max} of platelets: 730 nm. For light polarized parallel to the plane of the ray, (*c*) λ_{max} of platelets: 470 nm. For light polarized normal to the plane of the ray, (*d*) λ_{max} of platelets: 470 nm. For light polarized parallel to the plane of the ray. The vertical bars have been drawn on these charts to delimit the waveband thought to be useful for vision in *Trachurus*.

both planes of polarization, the layer reflects strongly at wavelengths of between 680 nm and 790 nm, but outside these wavelengths, the layer is almost transparent. As the angle of incidence increases, the reflecting wave-band shifts progressively to shorter wavelengths. Near the Brewster angle (which for a guanine–cytoplasm stack would be at around 53°) the layer becomes non-reflecting to light polarized parallel to the plane of the ray, whilst remaining highly reflecting for rays polarized normal to the plane of the ray, so light reflected by the layer is therefore highly polarized. At angles of incidence of greater than 70°, the layer becomes highly reflecting at all wavelengths, for both planes of polarization. Figures 13*c* and *d* show corresponding results for a stack with λ_{max} of 470 nm (at normal incidence).

(iii) *Superposed layers of platelets*

We shall now consider the reflective behaviour to be expected of multiple, superposed layers of platelets, such as those shown in figure 2*d* and *e*. When a fish is illuminated by highly directional light, such as sunlight or that used in the experimental conditions shown in figure 1, it is easy to observe the reflections from each layer almost independently of the other, merely by adjusting the angle of viewing. This is possible because the reflections are largely specular and the platelets of

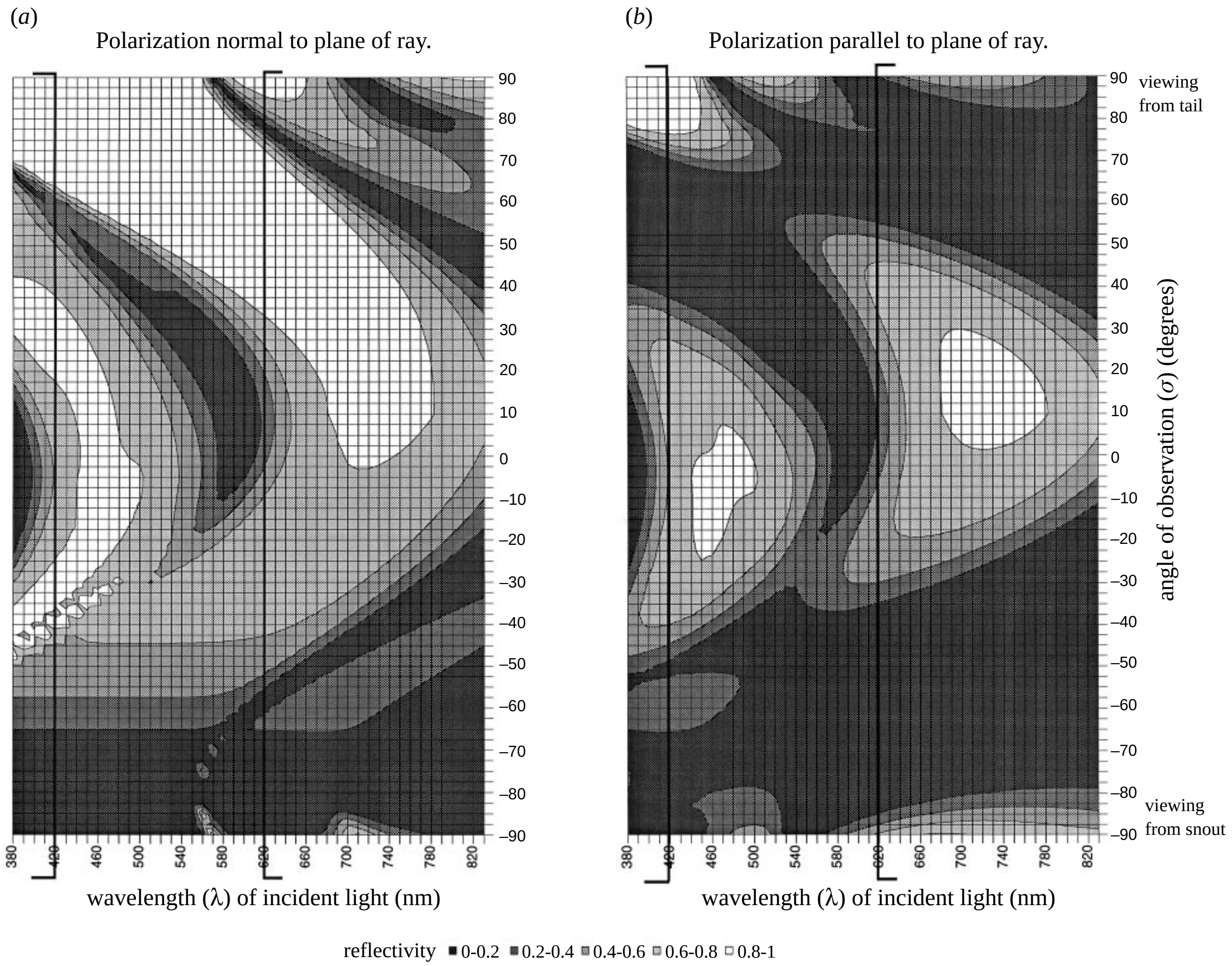


Figure 14. Calculated spectral reflectivities for a simple model of two layers of platelets (see the Appendix) at various wavelengths λ and at various angles of observation σ. The characteristics of the layers are assumed to be: outer (L) layer: $\lambda_{\max}$ of platelets: 730 nm, θ: 0°, ϵ: 10°; inner (S) layer: $\lambda_{\max}$ of platelets: 470 nm, θ: 0°, ϵ: -5°. The degree of shading at each point represents the reflectivity, such that light shading represents high reflectivity (and hence low transmission) and vice versa for dark shading. (*a*) For light polarized normal to the plane of the ray. (*b*) For light polarized parallel to the plane of the ray. The vertical bars have been drawn on these charts to delimit the waveband thought to be useful for vision in *Trachurus*.

the different layers are set at different angles relative to the surface of the fish. However, when we examine a fish in a light field such as that found under the sea, then no matter what direction we observe from, we will always see a superimposition of components reflected by both the L and S layers after originating from different directions in the field of light (figure 12*b*). We should expect the overall distributions of spectral reflectivity to approximate to a combination of pairs of reflections of the type shown in figures 13*a* with *c* and *b* with *d*. However, allowance must be made for the fact that light reflected by the inner (S) layer has passed through the outer (L) layer twice, possibly modifying its intensity and spectral composition. Furthermore, the two layers are neither parallel to one another, nor to the surface of the fish, then the distributions shown in figure 13*a* and *c*; and *b* and *d*, will be offset in the angle of incidence relative to one another and to the surface of the fish.

In figure 14*a* and *b*, we predict the spectral reflectivity of two superposed layers, again using Huxley's equations for the reflectivity of each layer, and using a simple model for the combining the effects of the two layers (see the Appendix for details). As in figure 12, the shading of each point in the chart areas shows the predicted reflectivity for that particular wavelength and angle of incidence. Since the physical arrangements are no longer completely symmetrical about the normal, both positive and negative angles of incidence are shown.

Figure 14 assumes the physical configuration shown in figure 12*b*; the observer is in a horizontal plane which contains the perpendicular to the surface in which the layers of platelets lie (see figure 12*b*), the external layer having $\lambda_{\max} = 730$ nm (at normal incidence) and the angular settings of $\theta_p = 0°$ and $\epsilon_p = 10°$, whilst the inner layer has $\lambda_{\max} = 470$ nm (at normal incidence) and the angular settings of $\theta_p = 0°$ and $\epsilon_p = -5°$.

In the upper half of each chart (i.e. viewing the fish from behind) the pattern of variation in reflectivity is close to a simple addition of figures 13*a* and *c* (for normal polarization) and figures 13*b* and *d* (for parallel polarization). This is because at wavelengths for which the inner (S) layer is strongly reflecting, the outer (L) layer is largely transparent and vice versa. The small

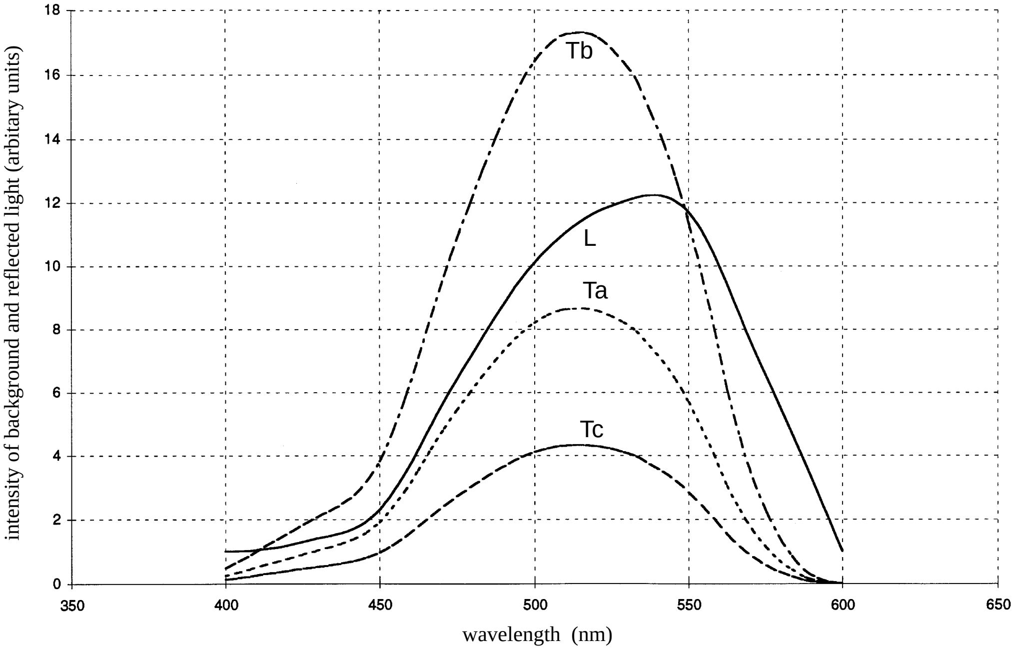


Figure 15. Diagram comparing the spectral characteristics of the background light in the sea (**L**) (solid line) and such light after reflection by a surface **T** (dashed lines) whose spectral reflectivity is given by the equations of Huxley (1968) for platelets with λ_{max}: 470 nm, and 0° angle of incidence. Curves are shown for three different angle of roll, θ. (**Ta**) $\theta_r = 0$; light reflected from the same level as the background light; (**Tb**) $\theta_r \approx +7°$; light reflected from a more upward direction, doubling its intensity; (**Tc**) $\theta_r \approx -7°$; light reflected from a more downward direction, halving its intensity.

vertical offset (i.e. in angle) between the patterns for the two layers is due to their differing values of ϵ.

In the lower half of each chart (i.e. viewing the fish from in front), the pattern initially approximates to a mirror image of the upper half, but at increasing angles of observation, the reflectivity tends to zero because the incident light is passing between the reflecting platelets and is lost in the interior of the fish (see the Appendix).

It is evident that the changes in spectral composition and intensity with angle of view are very much greater for such superposed layers than for the single layer of platelets.

(iv) *Effects of yawing, rolling, and pitching movements in the light distribution of the sea*

We may now consider the appearance of layers of platelets when viewed from a variety of angles and at various orientations in relation to the kind of light field within which the fish lives.

Suppose a reflecting surface **T** on a fish has a *single* layer of vertical platelets (figure 12*c*) and **T** is viewed by an observing fish, **O**, and imagine that **O** swims in a plane **V** parallel to **T** for which a perpendicular to **T** has a length **p** and intersects **V** at the point **P**. We can now draw circles around **P** defining positions on **V** for which the angles **OTP** are constant and for which the single layer of platelets will have the same spectral reflectivity. In figure 12*c*, we have indicated by such circles the positions for which σ is 0°, 20°, 30°, 40°, 50° and 60°. We can now, for a given type of platelet, predict the changes of spectral reflectivity of **T** for all positions of **O** in the plane **V**. (We note that, for a line such as **rr**', the angle σ cannot be less than the value σ_0 that it will have when the eye of **O** is in a plane perpendicular to **rr**' and containing **T**). Let us take as examples single layers of platelets for which the λ_{max} = 470 nm. From figure 13*a* and *c*, we see that, within the waveband $\lambda = 400$ to 620 nm (thought to contain the only useful light for the fish) then, for the layer of platelets $\lambda_{max} = 470$ nm, if $\sigma = 0°$ the reflectivity is high only in the band $\lambda = 440$ to 500 nm; when $\sigma = 30°$ only in the waveband $\lambda = 400$ to 480 nm and that when $\sigma = 50°$ only in the waveband $\lambda = 400$ to 420 nm. On figure 12*b*, the reflecting platelets are vertical, but in general, (see figure 2*b*, *c*) they will be set at an angle of θ_p to the vertical (positive values of θ meaning that the normal from the surface of the platelet inclines upward away from the fish). The **L** and **S** layers always also have different values of ϵ_p (the angles by which the platelets are tipped away from or towards the tail). It follows that, in general the brightness of the light reflected to the eye of an observer will be greater for one layer of platelets than for the other.

If the values of ϵ_p are different for the two layers, pitching will affect the relative contributions of the two layers to the reflected light. Thus, for the surfaces of a fish which has the disposition of platelets shown in figure (2*e*), when the fish dives the contribution of reflections of the **L** layer will become greater than those from the **S** layer. This is because platelets of the **L** layer are tipped about 20° more towards the tail. We may note that if the waveband being seen is one for which the sea absorbs light relatively heavily, the change in

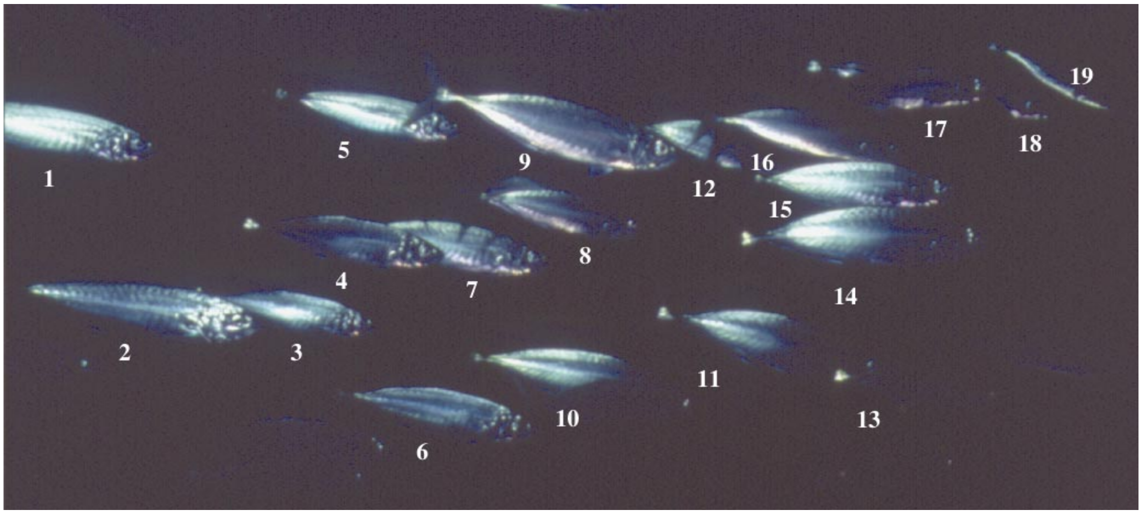


Figure 16. Photograph of a small school of *Decapterus koheru* taken in the sea by flash by Dr A. Rogers.

radiance with angle in the vertical plane will be greater than for wavebands to which the sea is less transparent (Duntley 1963; Timofeeva 1974). For the more heavily absorbed lights, the effects of rolling and pitching will, therefore, be greater.

(v) *The effects of rolling*

Suppose, for example, that the reflecting platelets in figure 12*c* have the optical properties illustrated in figure 13*c* and that **T** is perpendicular to the surface of the sea, and that **O** views **T** at normal incidence from point **P**. Then we see from figure 13 that the reflectivity of **T** is such that, for light in the waveband 440 to 500 nm, the light reflected to **O** will be such as to make **T** appear close in brightness to that of the background against which it is seen. In contrast, for light in the wavebands around 410 nm and around 550 nm (for which the reflectivity of **T** is around 50%), **T** will appear less bright than the background. To us, **T** would still appear blue.

Figure 15 shows predictions of the relative brightness of background and reflected light at different wavelengths for various angles of roll, θ_r. The background light is assumed to have the spectral characteristics typical of coastal waters and the reflected light is assumed to be this background light, reflected according to the equations of Huxley (1968). Curve **Ta** shows the predicted spectral characteristics of the light reflected by **T** under these conditions.

Suppose the fish now rolls so that the reflecting surface is turned upwards so as to reflect light from a direction from which the radiance is twice as great as that of the background, i.e. $\theta_r \approx +7°$ (curve **Tb** in figure 15). Then for the greater part of the waveband below 550 nm, the reflected light becomes almost twice as bright as the background, but for the waveband above 550 nm **T** remains less bright than the background.

If the fish rolls in the opposite sense so as to reflect light from a direction from which the radiance is half as great as that of the background, i.e. $\theta_r \approx -7°$), the fish will appear darker than the background for all of the spectrum. (curve **Tc** on figure 15). Remembering that reductions in brightness can be powerful visual stimuli, we see that if **O** has appropriate visual receptors, rolling of **T** will be strongly signalled as changes of brightness and colour. (The value $\theta_r = -7°$ is that found for area β on the ventral surfaces of the fish.)

If the area of the retina on which the image of the reflecting surface falls has only the one visual pigment, then, for angles of roll like that giving curve **Tb**, for one part of the spectrum the background will be brighter than the fish, whilst for another part of the spectrum, the fish will be brighter than the background; the two together will be closer to the background brightness than either on their own. This is because, for the two parts of the spectrum together, the number of quanta absorbed by the visual pigment per unit area will be closer to that for the background than for either part of the spectrum on its own. A change in the angle of roll will, however, cause both to change brightness in the same sense.

Similar conclusions may be drawn about the reflecting layers on the dorsal flanks of *Trachurus*; here Denton & Land (1971) found only a single layer of platelets reflecting best in the green but associated with pigments that moved the waveband maximally reflected into the blue. Here the platelets are inclined a few degrees upwards so that the less than 100% reflection of the incident light by the surface of the fish can be compensated for by the fish reflecting light from a more upward direction than the background.

(vi) *The answers to the questions*

We can now provide answers to the three questions posed under (i) above:

(a) the ability to produce and discriminate between different wavebands in the spectrum could increase the sensitivity of the reflector/visual system in the detection of movements;

(b) the L layer which reflects red light at normal incidence is useful because it reflects yellow to blue lights at oblique angles;

(c) two different layers set at different angles can give more dramatic and asymmetric changes in brightness and colour with changes in angles of viewing than single layers could do, and so allow small changes in roll, yaw and pitch to be easily detected and recognized.

Note: the angular distribution of light which has reached its asymptotic values depends on the relative degrees to which the light is absorbed and scattered, see Duntley (1963) and Timofeeva (1974); the greater the absorption the more pencil-like will be the polar distribution of light. Since scattering varies little with wavelength we should expect the radiance of light of the wavelengths which are more rapidly attenuated to change more quickly with changes of angle to the downwards vertical. This is a big effect; thus in clear oceanic waters, for a wavelength for which absorption is four times greater than that for the blue light which is best transmitted, the radiance doubles for every 7° change in angle towards the zenith instead of for every 20°.

(*e*) *An example*

Figure 16 is a remarkable photograph, of a small school of *Decapterus koheru* taken in the sea by Dr A. Rogers, showing almost all of the types of reflecting structures discussed above in one 'shot'. *Decapterus* is closely related to *Trachurus*, both being in the carangids in the same subfamily Caranginae. The individual fish have been given the numbers shown in the key.

We see:

(1) that particular surfaces of the fish that give bright reflections to the camera from one fish reflect little or no light from a neighbouring fish, showing that although the reflecting systems of such surfaces are not perfectly flat mirrors they generally only scatter the light falling on them over a small range of angles;

(2) that the tail spot, since it lies on the part of the fish that, when swimming, makes the largest lateral excursions and the largest changes of angle of attack, is the part for which the reflection of a directional source of light is the most variable in relation to the reflections from the rest of the fish. Compare, for example, fish 4 with fish 5; fishes 11 and 14 with fishes 15 and 16, and note fish 13 for which the tail spot is the only part of the fish giving a reflection in the direction of the camera;

(3) that for the fish on the left-hand side of the picture, e.g. fishes 1, 2, 3 and 4, the heads of the fish reflect much more strongly than they do on the right-hand side where they hardly gave any reflections at all. This is because the platelets on the head mostly have their surfaces tipped towards the snout whilst those of the body are tipped towards the tail;

(4) that for some fish, e.g. fishes 1 and 5, strong reflections are given by the main lateral-line canal whilst for others, e.g. fishes 9 and 10, strong reflections are given by the dorsal lateral-line canal;

(5) that in some fish, which are high in the field of the camera, the reflecting bands on the ventral surface of the fish are the only structures that are very visible, e.g. those of fish 19;

(6) that there are a number of areas behind and under the eye that differ markedly from one another in the spectral bands that they reflect the most strongly. See, for example, fishes 1, 3, 4 and 5. (From our observations, we think that the only reason why colours are not seen in fish 2 is that the colour film was over exposed by the strong reflections from these patches);

(7) that the colour of the ventral flank is sometimes green/blue and sometimes red—see fishes 9 and 6.

It must be stressed that the patterns of brightness and colour seen on the fish on figure 16 are not those which would be seen in the natural lighting found in the sea, as this photograph was taken with highly directional light from a flash. The interest of this photograph is in showing how directional the individual reflecting structures are.

(*f*) *Conclusion*

As we have argued in this and an earlier paper, the differences in the dispositions and spectral reflectivities of the reflecting platelets in different parts of the surfaces of the fish will produce large changes in the appearance of a fish to its neighbours when the fish rolls, yaws and pitches or changes its position with respect to its neighbours. This was confirmed by observations in the apparatus which simulated natural light in the sea.

Although the above account of the reflecting layers in the horse mackerel is far from being complete, it does indicate that the system is sophisticated and that its features accord well with the hypothesis that its main purpose is to signal the nature of any changing relations to the ambient light field produced by its own movements and to its relations to the positions of its neighbours produced by its own movements and those of its neighbours. We have not discussed the effects of the state of adaptation of the eye to various wavelengths of ambient light. It seems certain, however, that adaptation will increase the importance of light of wavelengths towards the limits set by the transmission of light by the sea.

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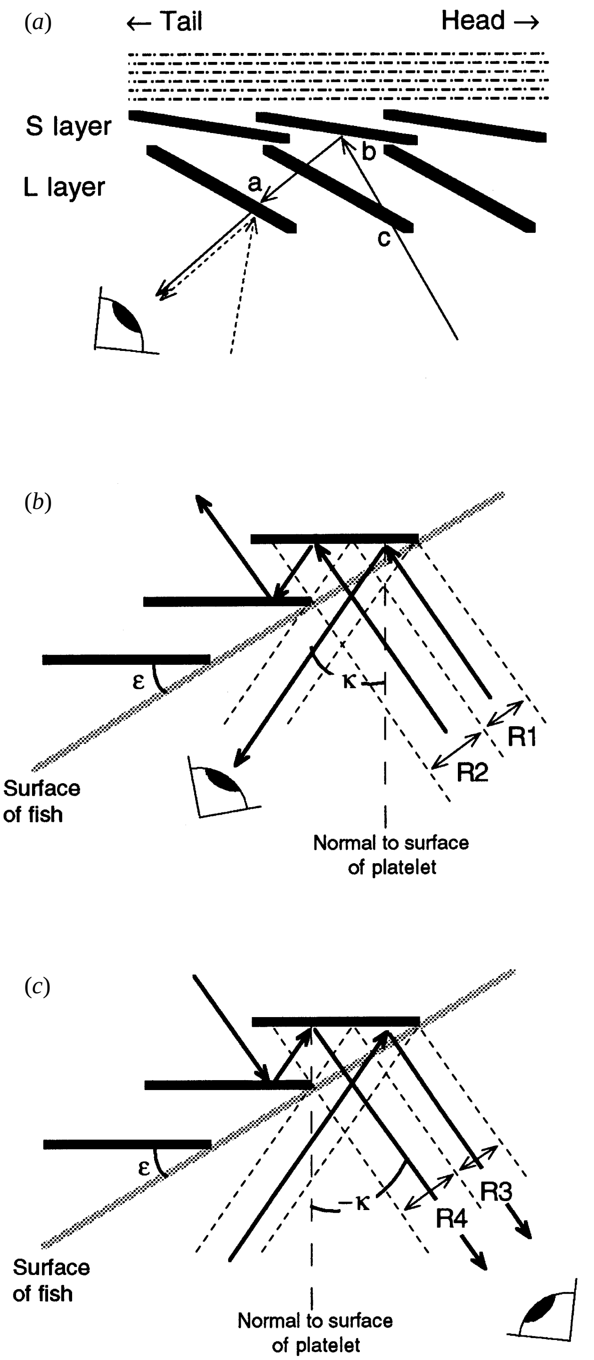

Figure 17. (*a*) Showing the configuration used for the calculations shown in figure 14. (*b*) Illustrating the way in which light is reflected and transmitted by platelets set at an angle to the surface of the fish $\epsilon \neq 0$, for positive angles of observation relative to the platelet (κ). (*c*) As for (*b*), but for negative angles of observation (κ).

APPENDIX

The following describes the method of calculation used to model superposed reflecting layers in figure 14.

It is assumed that light seen by the observer is the sum of two components (figure 17*a*). One component (dashed lines) has simply undergone one reflection by the **L** layer (e.g. at point **a**). The other component (solid lines) has passed through the **L** layer (e.g. at point **c**), undergone a reflection by the **S** layer (e.g. at point **b**) and has then passed back through the **L** layer (e.g. at point **a**). It is assumed that the spacing between the **L** and **S** layers is large enough and irregular enough for there to be no optical interference effects when combining the two components.

The reflecting elements of both the **L** and the **S** layers (shown as heavy solid bars) are assumed to be ideal, five-layer $\lambda/4$ stacks of guanine (refractive index = 1.83) separated by cytoplasm (refractive index = 1.33), with reflective properties given by the equations of Huxley (1968). Allowance is made for the fact that the platelets of each layer are rotated about a vertical axis relative to the surface of the fish (i.e. $\epsilon \neq 0$) (see figure

12*b*). Thus angles of incidence relative to the surface of the fish are offset from angles of incidence relative to the platelets (the latter determining the reflective properties of the platelets).

The rotation of the platelets about a vertical axis also gives rise to what may be described as 'Venetian Blind' effects, illustrated in figure 17*b* and *c*; these figures correspond to the horizontal plane of figure 12*b* but show only one layer of platelets. Note that the angle of observation σ in figure 12*b* is relative to the normal to the surface of the fish, whereas the corresponding angle κ of figure 17 is relative to the normal to the surface of the platelets; the difference between the two is ϵ.

In the case shown in figure 17*b*, incident light is split into two components: light passing through the regions such as R1 is reflected in the direction of the observer, whereas light passing through regions such as R2 passes between the platelets and so is available for reflection, scattering or absorption by internal layers. Although only part of the incident light flux is reflected towards the observer, the projected area of the surface of the fish in that direction is proportionally less than in the direction of the incident light, and so the intensity of the observed light is the same as that of the incident light (see Denton & Nicol (1966) for a fuller discussion, including the equations used here).

In the case shown in figure 17*c*, the observer sees a blend of light passing through regions such as R3 which is directly reflected incident light, and light passing through regions such as R4 which has been reflected or scattered by internal layers.

The limitations of this simple model are:

(i) It is assumed that light transmitted through the outer **L** layer passes through one platelet only; in reality, a ray may pass through a number of overlapping platelets, as shown near point **a** in figure 17*a*.

(ii) It is assumed that all reflecting platelets are vertical (i.e. $\theta_{\mathrm{p}} = 0$) and that the plane of observation is horizontal (as in figure 12*b*), so all incident light is similar; in reality, platelets may not be vertical, so the incident light may come from differing elevations and hence be of differing intensities and spectral composition.

(iii) It is assumed that all light incident on a layer is either reflected or transmitted; in reality, some light will be absorbed or scattered.

(iv) It is assumed that all light which passes through the inner **S** layer is lost; in reality, some light will be scattered by the underlying argenteum.

(v) It is assumed that light can only undergo a single reflection by the **S** layer; in reality, some light may undergo multiple reflections between the **S** and **L** layers.

(vi) It is assumed that light passing obliquely between platelets will undergo an even number of reflections (or none), and will continue in a direction parallel to its original course; in reality, some light will undergo an odd number of reflections and will change direction.