Bands against stripes on the backs of mackerel, *Scomber scombrus* L.

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A thin band of reflecting platelets overlies the central parts of the light and dark stripes found on each side of the dorsal surfaces of the body of the mackerel (*Scomber scombrus* L.). When this fish has its antero-posterior axis horizontal and its mid-dorsal and mid-ventral lines in the same vertical plane, V, the surfaces of the reflecting platelets in these bands are within a few degrees of being vertical. These surfaces are, however, tipped about 17° from plane V towards the tail. In the angular distributions of radiance commonly found in the sea, the reflections from these bands can mask parts of the pattern of light and dark stripes seen by neighbours in ways that depend on the orientation of the fish in the external light field and the position of the fish relative to its neighbours. With this arrangement, when the fish changes its orientation and/or its velocity with respect to neighbouring fish, this is signalled to its neighbours as changes in the patterns of brightness of its dorsal surfaces. Relatively small changes in roll, pitch and yaw can produce large changes in appearance and, as vision is a most important sense in the mackerel, it seems likely that these changes are important for signalling.

Keywords: communication between fish; fish, specialized reflectors; *Scomber*, light reflections; schooling in fish; reflective communication

1. INTRODUCTION

We have argued elsewhere (Denton & Rowe 1994) that silvery layers in the surfaces of schooling fish could be useful, both in making the fish less visible, (Franz 1907; Ward 1919; Denton 1970) and also in communicating information about the movements that a fish is making to its neighbours. The two functions need not be incompatible—a fish's surfaces may display a pattern of reflected light which by its size would be very visible to near neighbours, but which would not be resolved by more distant predators or prey. We have further showed that the horse mackerel has a number of specialized reflecting structures which can hardly fail to enhance the signalling process (Rowe & Denton 1997). Here we aim to show that the mackerel also has specialized reflecting structures with a similar purpose.

The stripes on the back of the mackerel are well known and it is tempting to think that in function they may resemble those of the zebra in acting as camouflage against a broken background. The mackerel is, however, a midwater fish and will not be viewed against such a background. However, animals commonly respond to moving stripes, so those of mackerel seem well-suited to playing a role in the signalling of movements between neighbouring fish in a school. Shaw & Tucker (1965) wrote 'the optomotor reflex may play an important role in schooling' and 'fish in the school may be providing a series of successive contrasts which are greatly enhanced because the fish are moving'.

Here we argue that the potential of the mackerel's stripes for communicating information about a fish's

movements is greatly enhanced by a thin layer of reflecting platelets overlying part of the striped region. To a neighbouring fish, light reflected by this layer will modify the view of the stripes in ways characteristic of the orientation of the fish, relative both to one another and to the ambient light field.

2. METHODS

Experimental work was done on mackerel, freshly killed by being placed in a suitable solution of the anaesthetic 2-methylbutan-2-ol (tertiary-amyl alcohol) until both respiratory movements of the operculi and reflexes had ceased for several minutes. Observations and measurements were made using two sets of apparatus.

1. Apparatus 1 for the angular dispositions of reflecting platelets (see Fig. 12 in Denton & Rowe 1994).
2. Apparatus 2, an improved version of that used by Denton & Rowe, to simulate the distribution of light radiance in the sea (Fig. 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 aluminium foil were laid against the surface of the fish to enable the angles of the surfaces to be determined. The platform holding the fish could be set at any desired angles of yaw, roll and pitch.

3. SYMBOLS

The effects to be described involve light from the natural field under the sea being reflected by one fish and

Figure 1. Diagram showing the three principal axes of the fish and angles of rotation about these axes, i.e. roll (ζ), pitch (ϕ) and yaw (ψ).

then observed by another. These effects will thus depend on the orientation of the observed fish relative to the light field and on the orientation of the observer relative to the observed fish. We define a reference position for the observed fish as being that of its normal swimming attitude (figure 1) with the its long axis horizontal and its mid-dorsal and mid-ventral lines in the same vertical plane V containing the x - and z -axes. In this reference position, the light field will be symmetrical about z .

In the experiments described, the observer and the observed fish were generally in the same horizontal plane, so we define their relative orientation in terms of the angle of observation between the line joining them and the y -axis of the fish at that time. We define the orientation of the fish relative to its reference position (hence relative to the light field) in terms of angles of roll (ζ), pitch (ϕ) and yaw (ψ).

The orientations of a reflecting surface with respect to the fish are described by the following symbols.

1. θ_p , the angle which a section through a platelet in a vertical plane perpendicular to V makes with a vertical line in this plane. For positive values, a normal to the reflecting surface is tipped upwards from the horizontal.
2. ϵ_p , the angle which a section through a platelet in a horizontal plane perpendicular to V makes with a horizontal line in this plane parallel to the long axis of the fish. For positive values, a normal to the reflecting surface is tipped towards the tail. (Diagrams illustrating this can be found in Denton & Rowe 1994.)

As mackerel taper towards the snout and tail, the surface containing the platelet is not necessarily parallel to the long axis of the fish. We therefore describe two further angles.

1. ϵ_t is the angle which a tangent to the surface of the fish makes with the long axis of the fish.
2. ϵ defines the orientation of a platelet with respect to the surface in which it lies. Therefore, $\epsilon = \epsilon_p - \epsilon_t$.

4. RESULTS

Figure 2a is a drawing of a side view of a mackerel showing the positions of some of the structures referred to in the text. When a mackerel was placed under seawater in a shallow dish, on a platform on which the fish could be rotated around its long, i.e. antero-posterior, axis, and

Figure 2. (a) Drawing of the side view of a mackerel (after Norman 1963) showing some of the structures referred to in the text: CB is a continuous narrow blue-black band, very close to the mid-dorsal line; DS is a region of dark stripes, which widen particularly at their lower ends. VF is the ventral flank, mostly covered with superposed layers of reflecting platelets, similar to those of the horse mackerel. (b) Enlarged view of the rectangular area in (a), observed from near the tail end of the fish. P indicates the reflecting band. (c) As (b), but observed from near the head end of the fish.

was then observed in direct sunlight. When the back of the fish faced the sun, the stripes on the dorsal surfaces could still be seen, but the areas between the stripes were almost as dark as the stripes themselves. When the fish on its side was viewed from a direction above and a little behind the fish, then, over most of the length of the fish's body, the central parts of the stripes were obscured by a bright reflecting band (figure 2b). When the fish was viewed on its side from a position ahead of the fish, the black stripes were very conspicuous against the areas between them, which were bright (figure 2c). Over a period of several months, we examined in this way at least 30 specimens with lengths of around 20–25 cm and the direction in which the stripes were visible or obscured varied little. This is consistent with our experience with other silvery fish for which we found that the patterns of reflective material varied little between individuals in the same age group.

Dissection showed that in this region of the fish (figures 3a,b), the visible stripes consist of a deep pigmented layer (M) external to which are reflecting bands containing iridiocytes (Ir) which scatter descending light sideways, more than upwards. (This is one reason why the areas between the black stripes are so much darker when the fish is viewed from above than when they are viewed from the side.) External to the central parts of the stripes, there is a layer, P, of reflecting platelets (Denton & Land 1970). These are much more specular reflectors than the iridiocytes. When it is illuminated by a parallel beam of light, almost all of the reflected light from layer P is contained in a cone with a semi-angle of about 5° .

Figure 3. Diagram of the rectangular area in figure 2*b,c* showing the relations between the black stripes (M), the iridescent reflectors (Ir) between the stripes, and the lower and upper parts of reflecting band, P1 and P2 for two different angles of viewing: (a) from towards the tail; and (b) from towards the head.

With apparatus 1, it was found that the surfaces of its platelets are almost perpendicular to the horizontal plane (θ_s around -2°). They are, however, tipped much more towards the tail, with $\epsilon=12^\circ$ (i.e. with respect to the surface of the fish) or $\epsilon_p \approx 17^\circ$ (i.e. with respect to the midline plane of the fish). The reflecting band (P) overlying the dorsal flank is coloured. In sunlight, at near-normal incidence, its lower part (P1) is yellow-green and its upper part (P2) is blue-green.

The ventral flanks (VF in figure 2*a*) are mostly covered with superposed layers of reflecting platelets, similar to those described for the horse mackerel by Rowe & Denton (1997). When illuminated with a parallel beam of light, these flanks appear bright red from some angles of view, and bright blue at other angles. Along the back, close to the mid-dorsal line, there is a thin blue-black reflecting layer (CB in figure 2*a*).

Fish were placed in seawater in apparatus 2 within which the angular distribution of light approximates to that found in the sea. Here the ways in which the patterns of reflection change with changes in the orientation of the fish were found. The fish were viewed with the eye of the observer in the same horizontal plane as the centre of the fish, or a little above or below this plane.

The platform holding the fish was of an appreciable size in relation to the size of the container; as a consequence, for the fish shown in the photographs of figures 4–7, 9 and 10, the angles of view varied along the fish. The values of yaw (ψ) given in the legends are those for the central position along the length of the fish. The values for ψ for the position of the foil (right-hand side of the centre) are all about 10° greater than those for the centre, whereas the

Figure 4. *Scomber scombrus*. Fish photographed in apparatus 2. The orientation of the fish was $\psi=60^\circ$, $\zeta=-17^\circ$, $\phi=-15^\circ$.

Figure 5. As figure 4, but with $\psi=59^\circ$, $\zeta=20^\circ$, $\phi=0^\circ$.

values for the cloth tape around the fish (left-hand side of centre) are all about 10° less.

Figure 4 shows the fish seen from the side and behind and a little above the fish, which has been subjected to a roll of -17° (i.e. with the side facing the observer rotated in a downward direction). The full extent of the striped area on the right-hand side of the fish can be seen. The reflecting band, P, although faint, is visible. It covers the central parts of the black stripes of the main part of the dorsal flank and almost all of the black stripes caudally from the strip of foil wrapped around the fish.

Figure 5 is similar to figure 4, but with zero roll. The reflecting band P obscures the central parts of the stripes almost completely at the tail end of the fish, but hardly affects them at all at the head end.

Figures 6 and 7 show some effects of change in yaw. For figure 6, the fish is in the reference position and is viewed from a point opposite the centre of its length. A strong reflection from the P band totally masks the parts of the dark and light stripes that lie under it. For figure 7, the fish is viewed from the side and head end of the fish. The band P is almost transparent and the full extent of the stripes can be seen. When the fish is viewed from the side and tail end of the fish, the band P again reflects light strongly and masks the central parts of the stripes. By direct observations, it was shown that, excluding angles close to glancing incidence, the black stripes of the region DS of figure 2 were almost equally dark across all of their width for angles of yaw more oblique than 35° towards the

Figure 6. As figure 4, but with $\psi=0^\circ$, $\zeta=0^\circ$, $\phi=0^\circ$ (the reference position).

Figure 7. As figure 4, but with $\psi=-40^\circ$, $\zeta=0^\circ$, $\phi=0^\circ$ (head towards the observer).

head and 60° towards the tail. Between these values, the central parts of the stripes were partly or (for most this angular range) fully obscured by the bright reflections of the band P.

Again, when a mackerel dives, the platelets of layer P on the fish's body which are tipped towards the tail, are turned to face in a more upward direction and so become brighter (figure 8). If the fish ascends, layer P on the body becomes darker. When the fish rolls, the whole side including the P band becomes brighter or less bright depending on whether the side faces in a more upward direction or reflects light from a more downward direction.

5. DISCUSSION

In addition to acting as reflectors, some layers of guanine crystals are used by fish to limit diffusion between neighbouring organs (Fänge 1958; Denton *et al.* 1972). Thus, in the conger eel, such layers are found around the swimbladder, the heart, the rete mirabile of the eyes and the abdominal cavity. In the swimbladder wall, large, extremely thin guanine crystals overlie each other so as to leave only narrow and tortuous liquid pathways along which diffusion can take place. These crystals slide against each other to accommodate changes in volume of the swimbladder. The reflectors of the bands which overlie the stripes on the backs of mackerel are not at all like this. In size, appearance and disposition, they are typical of the stacks of crystals and cytoplasmic spaces forming the platelets commonly found in fish reflectors.

Figure 8. As figure 4, but with $\psi=0^\circ$, $\zeta=0^\circ$, $\phi=20^\circ$.

These platelets give a high reflectivity of visible light with very small amounts of guanine. They are spaced apart from one another so that they cannot act as diffusion barriers, nor can they have an important mechanical role—a possibility for the argenteum of fish skins.

On the basis of measurements and observations of mackerel and other fish (see Denton & Land 1970; Rowe & Denton 1997), we can reasonably assume that the reflective units in the layer P are platelets consisting of approximately $\lambda/4$ stacks of guanine crystals and cytoplasm which, at normal incidence, reflect best in the blue-green parts of the spectrum for the upper part of the band, P2, and in the green-yellow in the lower part, P1.

From equations given by Huxley (1968), we have calculated (Rowe & Denton 1997), for various angles of observation, the spectral reflectivities of a single layer of platelets, all of which are ideal $\lambda/4$ stacks of five crystals separated by cytoplasm and which reflect maximally at the wavelength 520 nm at normal incidence. The platelets are assumed to have their vertical axis parallel to the plane of the surface in which they lie ($\theta=0^\circ$) and are tipped towards the tail ($\epsilon_p=17^\circ$). The latter case is that found in band P of the fish. The results of these calculations are shown in figure 9, which shows how reflectivity varies with wavelength and angle of observation. In this figure, areas of light shading indicate high reflectivity (and hence low transmission), and vice versa for dark shading. If we take an angle of observation of 12° (which represents the normal to the platelets), we can see that the platelets reflect strongly between the wavelengths 490 nm and 600 nm. As we observe from angles away from the normal to the platelets, the waveband for strongest reflectivity shifts towards shorter wavelengths. For angles of observation towards the snout, the reflectivity is sharply reduced owing to 'Venetian blind' effects, in which light travelling nearly parallel to the platelets passes between them, rather than being reflected by them (see figure 10*b* and Rowe & Denton 1997). At angles of observation between about 60° and 80° , the reflectivity is reduced because only light with its plane of polarization normal to the plane of the ray is reflected. As the angle of observation approaches 90° , the platelets become highly reflective at all wavelengths and for all planes of polarization.

We therefore see that the idealized band P would reflect blue-green light, strongly between the angles of observation of 60° towards the tail, and 30° towards the head;

Figure 9. Calculated spectral reflectivities of a single layer of platelets at various wavelengths, λ , and at various angles of observation. Each platelet is assumed to be an ideal $\lambda/4$ stack of five guanine crystals separated by cytoplasm with a $\lambda_{\max}$ of 520 nm. The angular orientation of the platelets is θ , 0° ; ϵ , 12° . 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. The reflectivities for the two planes of polarization have been averaged.

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Figure 10. Diagrams showing the angular ranges over which particular factors are important in determining the reflectivity of the dorsal and dorso-lateral areas of the surfaces of the mackerel. (a) The upper part of a vertical cross-section through the post-abdominal region of the fish. (b) A horizontal section passing through the upper part of the fish in the centre of the stripes. The regions marked A contain the angles of observation for which the band P (see figure 2*b, c*) reflects mainly in the blue and green parts of the spectrum, while the regions marked B are those for which the reflections are mainly in the near UV. The regions marked VB are those for which the 'Venetian Blind' effect applies. SPA is a region from which the projected area of the plate P is very small or absent.

these values are in reasonable agreement with those found experimentally. As we move outside these angles, P would become more and more transparent to light in the waveband between $\lambda=400$ nm and $\lambda=600$ nm. At oblique angles of incidence, it would reflect strongly in the near ultraviolet (UV); this is a waveband which neither older mackerel nor humans can see, because the lenses in the eyes of both older mackerel and humans do not transmit light in the near UV (Thorpe & Douglas 1993). The light that is strongly reflected at lower angles of incidence is in the waveband to which the sea is most transparent. It is also the waveband to which the eyes of fish like the mackerel are, as judged from their visual pigments, most sensitive (Partridge 1990).

When we consider the visibility of a given element of the surface of a fish from a particular direction, we must also take into account projected area effects (Denton &

Figure 11. *Scomber scombrus*. Diagrams showing the appearance of the dorsal flank of one fish T to the eye of another fish O. (a) A horizontal section through the fish at the level of band P showing the line β at an angle of observation of 60° towards the tail. For angles $< 60^\circ$ (for example, α), the stripes are visible (SV); for angles $> 60^\circ$ (for example, γ) the stripes are obscured (SO) by the reflections of band P. (b) The fish T is viewed from positions O₁, O₂ and O₃. (c) Shows the appearance of fish T from positions O₁, O₂ and O₃ of (b). Note that no corrections have been made for the differences in distance between the eye of O and the fish T.

Nicol 1966). Figure 10 illustrates some of the effects described in the previous paragraph. Figure 10a shows a vertical cross-section of a mackerel in the post-abdominal region. The platelets of the band P are shown greatly enlarged; in reality, they are only about $5\mu\text{m}$ high. The positions from which the band P either cannot, or can hardly, be seen at all are labelled SPA (for small or zero projected-area). The positions from which the reflections of band P are lost in the pigment layers below the band

are labelled VB (for Venetian Blind). In between these two zones, the regions marked A are those from which the reflections are in the visible parts of the spectrum, and B are those from which the reflections are mainly in the near UV.

Figure 10b shows a horizontal section through the fish passing through the upper part of the body in the region of the stripes. Areas with reflective properties similar to those in figure 10a are shown.

To fully understand the ways in which the pattern of stripes would appear in the sea to a neighbouring fish from different points of view, we would have to take into account the availability of lights of different parts of the spectrum, the degrees and directions to which the light is polarized, and the properties of the visual system of this fish. However, it is clear that the presence of the layer P will make the changes in pattern with changes in the relative positions of fish more dramatic than they would otherwise be.

We can illustrate this with an example: suppose that a fish O observes a fish T at a distance of about half of a fish length (figure 11). The pattern of stripes and dashes seen by O on the dorsal regions of T will, for some angles of observation, change in a very striking way for small changes in this angle, particularly at approximately 60° towards the tail and at approximately 30° towards the head. Figure 11a shows how, from one point of observation, some regions of T will have the stripes obscured and others will have the stripes visible. Now suppose that O swims forward relative to T (figure 11b); for O, the boundary between the obscured and visible stripes on T will move forward (figure 11c). Equally great changes would be given by small variations in the angle of yaw (ψ) of T. Thus, changes of $\pm 10^\circ$ in yaw will have effects of similar magnitude to those given by fish O moving between positions O₁, O₂ and O₃. We note that the visual effects on the appearance of T to O are quite different for yaws of T and yaws of O. Yawing of T will produce substantial changes in the pattern of stimulation of the receptors in the retina of the left eye of O, with only a small change in the position of the image on the retina. In contrast, yawing of O will give only small changes in the pattern of stimulation of its retina, but large changes in the position of the stimulation of the retina.

So far in this paper we have considered only one of the mackerel's specialized reflecting systems, whose appearance depends on the relative positions of the observed and observing fish. Over great parts of its ventral flanks, the mackerel has several superposed layers of reflecting platelets, which differ greatly from each other in their spectral reflectivities and in their orientations. Very similar layers are found in the corresponding regions of the surfaces of the horse mackerel; these have been studied by Rowe & Denton (1997). They have shown that, when viewed in light fields such as those found in the sea, the patterns of light reflected will change greatly in intensity, spectral composition and polarization with the direction and distance of the observer and the orientation of the fish in the ambient light field. The changes are particularly sharp at angles of observation of approximately 50° towards the tail (Rowe & Denton 1997, Fig. 14).

At the head end of the ventral surfaces, there are also two superposed layers of platelets with differing reflectivities, but these platelets are tipped towards the snout rather than the tail, and so the distinctive changes in appearance of these areas occur when viewed from positions ahead of the fish rather than behind it.

If there are optimal spatial relations between fish giving the most economical swimming (Weihs 1973) or the best disposition for escaping from predators, it would be advantageous if the patterns of brightness of the surfaces of the fish changed quickly with changes of

angles of observation at these optimal angles. However, there is no consensus among those who have studied the spatial relations of fish in schools. It does seem certain that these relations certainly change with the activity of the school—including migrating, feeding and avoiding predators (for an excellent review, see Pitcher & Parrish 1993). A further uncertainty lies in the fact that laboratory experiments on schooling have not been made with angular distributions of radiance and spectral distributions close to those found in the sea. Pitcher & Parrish note that fish in the wild often exhibit remarkably regular three-dimensional spacing.

The combination of an external silvery layer overlying a series of dark and light stripes which we have described here is not unique to the mackerel, and we have seen very similar arrangements in barracuda. In the absence of behavioural studies, we cannot be certain of the exact roles which the silvery layers play in the lives of either mackerel or horse mackerel. However, these reflecting layers play such a main role in determining the appearance of the fish, ensuring that this changes greatly with changes in the direction of view (as would be observed by neighbouring fish in a school), that they must give their possessors considerable advantages in being able to react quickly while schooling and feeding.

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