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THE STRUCTURAL BASIS FOR IRIDESCENT COLOUR CHANGES IN DERMAL AND CORNEAL IRIDOPHORES IN FISH

BY J. N. LYTHGOE AND JULIA SHAND

Department of Zoology, University of Bristol, Woodland Road, Bristol BS8 1UG, UK

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Summary

The reflectance from the iridophores in the skin of the neon tetra *Paracheirodon innesi* (Myers) and the iridophores in the cornea of the sand goby *Pomatoschistus minutus* (Pallas) changes in response to light. In both cases the reflectance comes from the constructive interference of alternating plates of material of high and low refractive index. In the neon tetra the high refractive index plates are mainly guanine, and the low refractive index plates are cytoplasm. In the goby cornea the plates are made of intercellular matrix and cytoplasm, but it is not known which has the higher refractive index. In neon tetra dermal iridophores, the response to light is a shift to longer wavelength reflection without an accompanying increase in the amplitude of reflectance. In goby cornea, light can induce an increase in the amplitude of reflectance without a shift in wavelength. It is suggested that the wavelength shift is produced by an inflow of material into the iridophore and that the change in amplitude, without a shift in wavelength, is produced by a transfer of material, such as water, between the high and low refractive index layers of the multilayer stack.

Introduction

In some fish (Clothier & Lythgoe, 1987; Oshima *et al.* 1985) and at least one cephalopod (Young & Arnold, 1982), the colour of light reflected from the iridophores is under physiological control. In each case the reflecting layer is constructed from a regular stack of very thin transparent plates of alternately high and low refractive index. Light is reflected at each refractive index boundary, and the whole stack reflects light within particular wavelength bands by the process of constructive interference. Those wavelengths that are not reflected are transmitted. The colour of the reflected light depends upon the thickness of the plates, their refractive indices and the angle of incidence of the light. In biological systems it is probably changes in the thickness of the plates that are most often responsible for changes in colour.

Huxley (1968) has given us a comprehensive mathematical model for the

Key words: iridophores, *Paracheirodon*, *Pomatoschistus*, cornea, light, colour change.

iridescent reflections from biological systems and Land (1972) has set out the most relevant points in a manner that is accessible to biologists. Using Huxley's model it is possible to calculate a complete spectral reflectance curve, at all angles of incident light, for any stack of alternating plates of different refractive index, provided the refractive index, thickness and number of plates are known. The actual shape and amplitude of the spectral reflectance curve depends upon all the variables mentioned above and such curves are helpful in trying to understand the structures that are involved in iridescent reflections. This is particularly useful in situations where the layers are too thin to be resolved by light microscopy and avoids the notorious difficulty of preserving absolute dimensions in tissue prepared for electron microscopy. In this paper we show how the characteristic differences in spectral reflectance changes in neon tetra skin and goby cornea can be explained on anatomical and physiological bases.

Physiologically active iridophores of the neon tetra are present in the brilliantly iridescent lateral stripe that runs along the body from the eye to the base of the tail. In daylight or when the fish is aroused the stripe is green or blue-green in colour, but at night the wavelength of light reflected shifts from the green, through blue to violet and ultimately to the ultraviolet. The structure (Fig. 1A) and reflecting properties of the iridophore have been described by Lythgoe & Shand

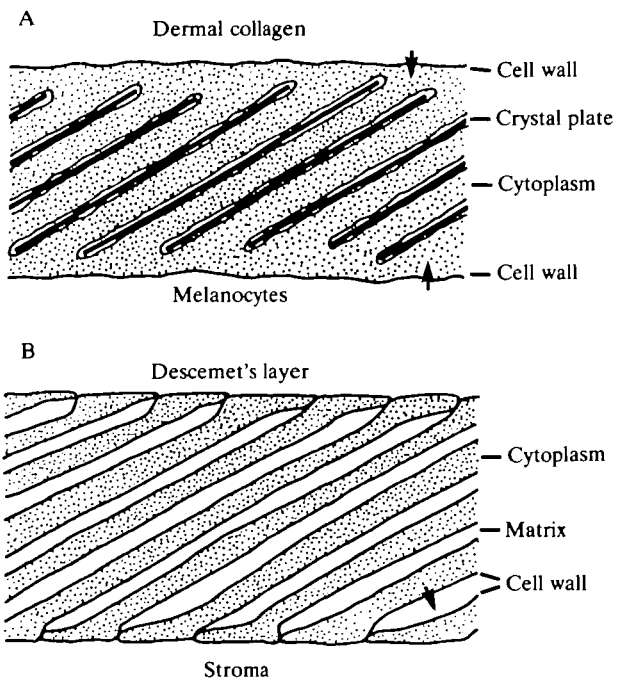

Fig. 1. Diagram of part of a section of a dermal iridophore of the neon tetra (A), and a composite iridophore in the cornea of the goby (B). The arrows cross the membranes which are believed to be involved in the transport of material during light- and dark-induced changes in reflectance.

(1982). The high refractive index layers are thin intracellular crystals which contain a large proportion of guanine (Land, 1972) and, judging from their shape, probably also contain a proportion of hypoxanthine (Greenstein, 1966). Each crystal is a broad hexagon and is less than about 20 nm thick. Between each crystal is a sheet of cytoplasm, between 100 and 200 nm thick, depending on its physiological state. The multilayer stack within each iridophore contains about 20 crystal and cytoplasm pairs. An important stimulus for the colour change is a rise or fall in light intensity on the iridophore itself and it is interesting that immunocytochemical studies reveal the presence of a rhodopsin-like molecule within the iridophore (Lythgoe *et al.* 1984).

Many diurnal shallow-living marine fishes have iridescent corneas. At least seven distinct anatomical structures are responsible in different species (Lythgoe, 1975; Shand, 1988) and four of these layer types are known to be physiologically active. When the colour changes in response to light, it is in the same direction as for neon tetra skin, from short to longer wavelengths (Shand & Lythgoe, 1987; Shand, 1988). Perhaps the most common light-activated type of corneal iridophore is that possessed by gobies and many other percomorphid fishes. The reflecting stack (Fig. 1B) is constructed of very thin whole cells separated by an extracellular matrix with little fine structure that we can discern by electron microscopy.

It is generally agreed that the colour shift in fish dermal iridescence is due to an increase in the thickness of the cytoplasm layers, with no corresponding increase in the thickness of the crystal plates (Foster, 1933, 1937; Rohrlich, 1974; Lythgoe & Shand, 1982; Oshima *et al.* 1985; Clothier & Lythgoe, 1987). A colour change in corneal iridescence can also be explained by postulating a change in the thickness of the cytoplasm layers or the matrix layers, or both. However, in the sand goby *Pomatoschistus minutus* light causes an increase in the amplitude of the reflection from the cornea, often without any change in its colour, and this is difficult to explain by postulating an increase in the total thickness of the layer pairs. We believe that this is the first time that this type of iridescent reflection change has been reported and we think it can be explained by postulating a transfer of material, perhaps water, between the cytoplasm and matrix layers with no net transfer between the iridescent layer and the tissues adjacent to it.

The value to the fish of these light-induced changes in reflection are a matter of conjecture. Lythgoe (1975) has suggested that the goby cornea acts as a sophisticated sunshade whereby the rays of the sun that shine on the cornea from above are reflected away, but the image-forming rays from objects in the water which arrive from a more horizontal direction are allowed to pass through. In the case of the neon tetra, it is supposed that the brilliantly iridescent lateral stripe together with its conspicuous ventral red pigment coloration acts as some kind of social marker to others of the same species. At night, neon tetras lie unmoving on the bottom, the red and black chromatophores contract and the reflections of the structural colours move into the ultraviolet (Lythgoe & Shand, 1983). There is, however, some need for caution in attributing the iridescent colour change to a need to be inconspicuous at night, for it is known that at least some shallow-living

teleost fishes can see into the ultraviolet (see Bowmaker & Kunz, 1987, for a review). Whether the potential predators on neon tetras can detect the ultraviolet reflections in the prevailing light conditions in the shallow waters of the Amazon basin at night remains to be seen.

Materials and methods

Neon tetras, *Paracheirodon innesi*, were purchased from a supplier of aquarium fish who had imported them from commercial breeders in southeast Asia. They were maintained at 23°C, on a 12 h:12 h light:dark regime. Sand gobies, *Pomatoschistus minutus*, were caught by beam trawling in shallow water in the Plymouth area of southwest England. In Bristol they were maintained at 14°C under natural light conditions.

Preparation

Neon tetras were decapitated and pinned, through the caudal peduncle and pectoral girdle, to a layer of wax in a Petri dish containing phosphate-buffered saline (PBS) (Oxoid, Dulbecco A, pH 7·3, diluted to 138 mosmol kg^{-1}). Gobies were decapitated, enucleated and the eye positioned cornea upwards in a Petri dish containing PBS (diluted to 227 mosmol kg^{-1}). The preparations were placed on the stage of an Olympus BHA microscope fitted with a 10× glass objective and an Olympus PM6 camera. The area measured was a spot of approximately 0·5 mm in diameter.

Spectral reflectance measurements

The photomultiplier head of a Macam SR3000 scanning spectroradiometer was connected to the exposure meter port of the microscope camera by a light guide. The specimen was illuminated from the angle giving maximum reflection (approximately 45° to the dorsal–ventral axis) by a Schott quartz–halogen (15 V, 150 W) lamp with a Hoya 80A blue-transmitting filter in the light path. The procedure for calibrating the intensity of the light was the same as that detailed by Clothier & Lythgoe (1987). The intensity at the level of the specimen was approximately 1×10^{19} photons $m^{-2}\,s^{-1}$. The apparatus was calibrated by reference to polished aluminium foil which has an almost flat spectral reflectance curve in the visible spectrum (Wyszecki & Stiles, 1967).

Once the preparation had been set up measurements were taken at 2 min intervals, until the reflectance fluctuations had stabilized, which took approximately 15–20 min. The measuring and room lights were then switched off for 2 h. Following the period of dark adaptation the measuring light was turned on and repeat records of spectral reflectance were taken at intervals of 1 min thereafter. Each scan, between 390 and 700 nm, took approximately 20 s to complete and the data were recorded on an x–y chart recorder. Room temperature was maintained at 20–23°C for experiments with the neon tetras and 17–20°C for the gobies.

Results

The spectral reflectance curves from neon tetra lateral stripe and goby cornea are shown in Figs 2, 3A–C. For both dermal and corneal iridophores the spectral reflectance prior to the dark period is redder than that observed in placid living fish, probably due to the stress involved in taking them from the holding tank. The shift to shorter wavelengths after the initial stress-related reddening is similar in both cases. However, in the neon tetra a period in the dark resulted in a shift in spectral reflectance into the violet and ultraviolet without much change in amplitude. The response to light involved a shift in spectral reflectance back from a reflectance maximum (R_{max}) at 400 nm or less to an R_{max} at around 480 nm (Fig. 2). After a further period in the light there was a slight shift in R_{max} back to shorter wavelengths as reported by Lythgoe & Shand (1982).

In goby cornea there was a similar initial light-adapted shift to shorter wavelengths as occurs in the neon tetra, but we never observed the dark-adapted R_{max} extending into the ultraviolet (Fig. 3A–C). The recovery of iridescence after the period of dark adaptation was different from that observed in the neon tetra in that there was always a strong increase in the amplitude of reflection, sometimes (as in Fig. 3A,B) with no accompanying increase in wavelength.

Discussion

All the investigators cited below agree that the change in colour of the

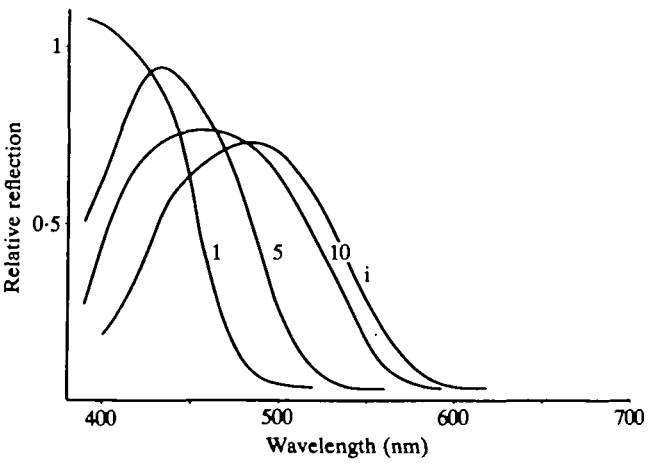

Fig. 2. Changes in spectral reflectance of the neon tetra dermal iridophore in response to light. The initial (i) curve is the spectral reflectance before a 2 h dark adaptation period. 1, 5, and 10 refer to minutes in the light after the period of dark adaptation. Note there is a shift to longer wavelengths which is produced by an increase in the thickness of cytoplasm separating the crystal plates. The reduction in the amplitude of reflection at longer wavelengths may be partly because the optical thickness of the guanine plates (although not their actual thickness) is reduced as the optical thickness of the cytoplasmic plates increases.

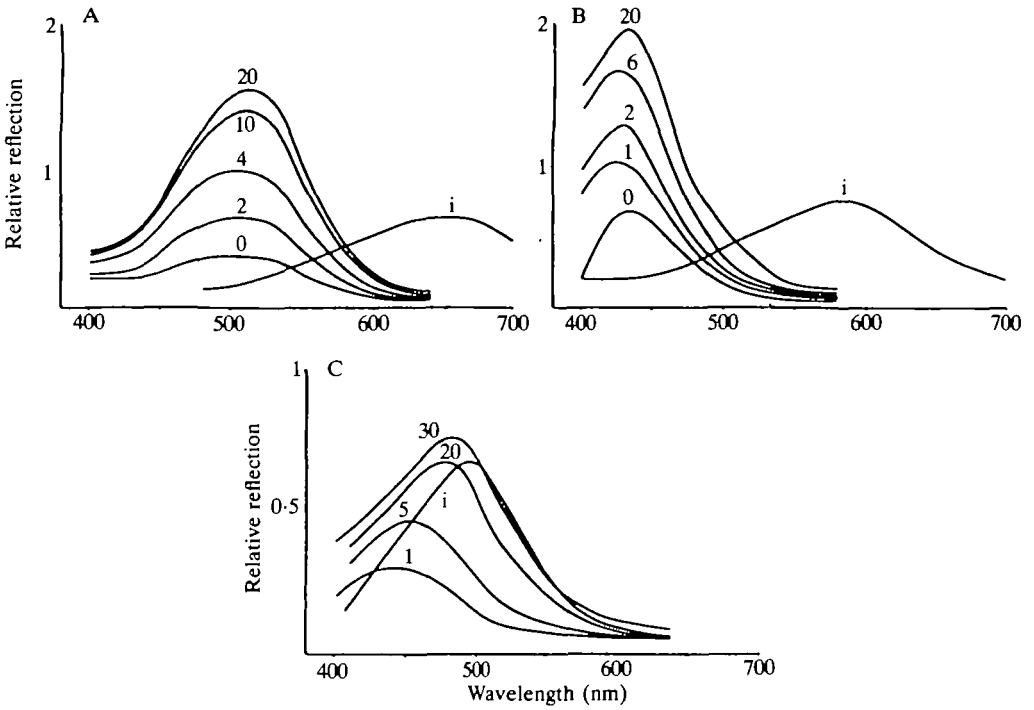

Fig. 3. (A–C) Changes in spectral reflectance from the cornea of the sand goby in response to light. Each set of curves refers to an individual fish. The initial (*i*) curves are for the light-adapted cornea before the 2 h period of dark adaptation began. The numbers refer to the time in minutes in the light after the period of dark adaptation. Note that there can be increases in the amplitude of reflectance with little or no shift in wavelength (A,B) which may be due to a transfer of material between the plates of high and low refractive index. The long-wavelength reflectance at the beginning of the experiment may be a result of an inflow of material into the iridophore which accompanies the stress of capture. For the values in Table 1, the model does not predict the low amplitude of reflectance in the initial curves.

physiologically active dermal iridophores of fishes can be explained by a change in the thickness of the cytoplasm layers in the iridophore, but there is a difference of view concerning the mechanism controlling the change in thickness. Rohrlich (1974), Kasukawa *et al.* (1986) and Oshima *et al.* (1985) think that the microfilaments and microtubules observed in the cytoplasm layers are likely to be involved in the change in thickness of those layers. However Foster (1933, 1937), Lythgoe & Shand (1982) and Clothier & Lythgoe (1987) think that the mechanism is likely to be driven primarily by the opening and closing of ion gates in the cell plasma membrane, resulting in water moving across the membrane. Either explanation could be correct for the measured reflectance changes in neon tetra iridophores, but we think it is easier to explain the reflectance changes in goby cornea by the movement of ions and water across membranes.

Using Huxley's model, the effect of changing the thickness of the cytoplasm

layer alone can be predicted (Table 1A; Fig. 4). The shift in reflection to longer wavelengths is well illustrated. The computed curves are narrower than the measured ones from the neon tetra skin, which may be partly because individual iridophores differ slightly in colour across their surface and partly because there are differences in colour between neighbouring iridophores. The model ignores intracellular membranes and other structures which may give discontinuities in refractive index that may also broaden the measured spectral reflectance curves.

A characteristic of our measured reflectance curves for the neon tetra skin is that the longer-wavelength curves are broader than those at shorter wavelengths and the amplitude of R_{max} is reduced (Fig. 2). In part this is because the ratio of the optical thicknesses of the crystal plate and the cytoplasm layers reduces as the cytoplasm layers swell and the crystal plates do not. It may also be that the range of reflected colours is greater for long-wavelength reflecting cells, which would have the effect of broadening the long-wavelength reflectance curves and reducing the R_{max}.

The goby cornea often shows large changes in R_{max} with negligible changes in wavelength (Fig. 3A–C). One explanation for this might be that there is a change in the number of reflecting plates; but since each cytoplasmic layer is a whole cell, it is difficult to see how there can be a change in the number of reflecting layers within the few minutes required for the reflectance changes to occur. We think it is more likely that there is a transfer of material between the two reflecting layers of the corneal iridophores and such a mechanism can be predicted by the Huxley model to alter the amplitude of reflectance without changing its wavelength.

Land (1972) has shown how the Huxley (1968) model predicts that if the optical thickness (the product of the actual thickness and the refractive index) of one layer is less than about 25 % of the combined optical thickness of the two layers, then R_{max} is small. R_{max} is also reduced when the difference between the refractive

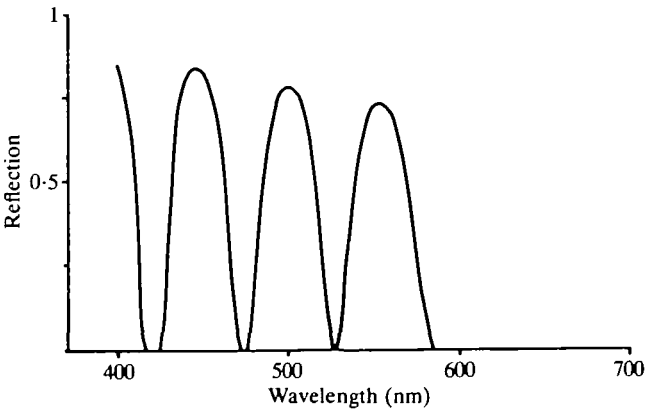

Fig. 4. Computed spectral reflectance curves (harmonic side bands ignored) for neon tetra iridophores having the refractive index and values shown in Table 1A. The thickness and refractive index of the crystal plates do not change; water enters the cytoplasm layers.

Table 1. *The data used to calculate the spectral reflectance curves shown in Figs 4–7*

Crystal plate		Cytoplasm			
Nb	Db	Na	Da	λR_{max}	R_{max}
(A) *Neon tetra (Fig. 4). Crystal plates do not change, water flows into the cytoplasm of the iridophore.*					
1·83	10	1·37	130	393	0·90
1·83	10	1·364	150	446	0·83
1·83	10	1·361	170	499	0·77
1·83	10	1·357	190	552	0·72
Intercellular matrix		**Cytoplasm**			
Na	Da	Nb	Db	λR_{max}	R_{max}
(B) *Goby cornea (Fig. 5). Refractive index of intercellular matrix low compared to that of the cytoplasm. No inflow of water into the iridophore.*					
1·33	10	1·377	145	426	0·04
1·33	20	1·381	135	426	0·17
1·33	40	1·39	115	426	0·53
1·33	55	1·40	100	426	0·77
Nb	Db	Na	Da	λR_{max}	R_{max}
(C) *Goby cornea (Fig. 6). Refractive index of intercellular matrix high compared to cytoplasm. No inflow of water into the iridophore.*					
1·55	10	1·338	175	499	0·48
1·385	40	1·339	145	499	0·33
1·374	50	1·34	135	499	0·27
1·361	70	1·342	115	499	0·14
1·354	90	1·344	95	499	0·05
Na	Da	Nb	Db	λR_{max}	R_{max}
(D) *Goby cornea (Fig. 7). Water flows into matrix and cytoplasm equally.*					
1·33	15	1·376	150	453	0·08
1·33	20	1·375	155	479	0·11
1·33	30	1·372	165	533	0·16
1·33	40	1·367	185	612	0·16

There are 20 layer pairs in the neon tetra dermal iridophores, and 30 layer pairs in goby cornea. It is assumed that the mobile material is water of refractive index 1·33.

Na and Da are the refractive index and thickness (nm) of the low refractive index layers; Nb and Db are the refractive index and thickness of the high refractive index layers. λR_{max} is the wavelength of maximum reflectance (nm) and R_{max} is the proportion of light reflected at λR_{max}.

indices of the two types of layer is reduced. If the iridophore acts as a closed system with transport of material across the membranes separating the two types of layer, we argue below that there will be a shift in the amplitude of reflectance without a shift in wavelength. This situation is modelled in Figs 5 and 6 using data contained in Table 1B,C, and could explain the experimental data shown in Fig. 3A–C.

The wavelength of maximum reflection (λR_{max}) from a regular multilayer stack of thin films is given by:

$$\lambda R_{max} = 2(Na \cdot Da + Nb \cdot Db) , \quad (1)$$

where Na and Nb are the refractive indices of the low and high refractive index

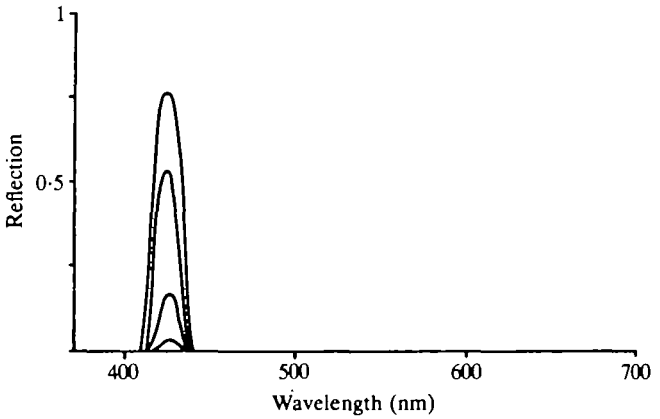

Fig. 5. Computed spectral reflectance curves for goby cornea. Values for the refractive index and thickness of the plates are shown in Table 1B. Water travels between low refractive index matrix and higher refractive index cytoplasm. No net flow of water in or out of the iridophore.

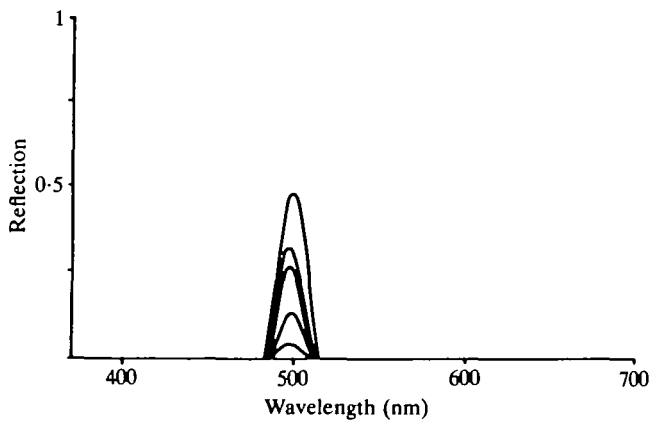

Fig. 6. Computed spectral reflectance curves for goby cornea. Values for the refractive index and thickness of the plates are shown in Table 1C. Water travels between lower refractive index cytoplasm and higher refractive index matrix. No net flow of water in or out of the iridophore.

layers, respectively, and Da and Db are the thicknesses of the two layers, respectively.

If there is no change in the wavelength of reflectance following the transfer of material between the two types of layer, then:

$$[Na(m) \cdot Da(m) + Nb \cdot Db] = [Na \cdot Da + Nb(m) \cdot Db(m)] . \quad (2)$$

m indicates where the values for the thickness and refractive index of the layer have been changed by the presence of the mobile material which has a refractive index of Nm and occupies an equivalent thickness of Dm.

The thicknesses of the matrix and cytoplasm layers are given by:

$$Da(m) = Da + Dm \quad (3)$$

and

$$Db(m) = Db + Dm . \quad (4)$$

If it is assumed that the refractive index of the layers changed by the presence of the mobile material is proportional to the concentration of dissolved material, the refractive indices of each layer are:

$$Na(m) = (Dm \cdot Nm + Na \cdot Da)/(Dm + Da) \quad (5)$$

and

$$Nb(m) = (Dm \cdot Nm + Nb \cdot Db)/(Dm + Db) . \quad (6)$$

By substituting the values on the right-hand side of equations 3, 5 and 6 into equation 2, it is evident that equation 2 is true and the movement of material between plates causes no change in the wavelength of maximum reflection. However, the amplitude of the reflected light is reduced when the optical thickness of one of the layers is less than about 25 % of the sum of the optical thicknesses of the two layers (Land, 1972). Land also points out that the harmonic side bands can become significant when one layer is relatively thin, but this does not seem to be the case for either neon tetra skin or goby cornea.

Like the dermal iridophores, the reflectance changes shown by goby cornea can be explained by the passage of a material such as water across the cell plasma membrane. An important difference between the goby cornea iridophores and the neon tetra skin iridophores is that the cytoplasm layers in the corneal iridophores are whole cells which are separated by apparently amorphous matrix material (Fig. 1A,B). In this case transport of material across the cell plasma membranes need not involve any transport into or out of the iridophore, but rather a redistribution of material within it. This is the situation envisaged in equations 1–6 (Figs 5, 6). The slight shift to longer wavelengths that often accompanies illumination (Fig. 3C) and the large shift that accompanies stress in the living fish can be explained by supposing that there is an inflow of material from the collagen stroma and Descemets layer into the iridophore. This situation is modelled in Table 1D and Fig. 7.

The change in the amplitude of R_{max} as modelled in Figs 5 and 6 can be explained either by a change in the optical thickness of one layer compared to the

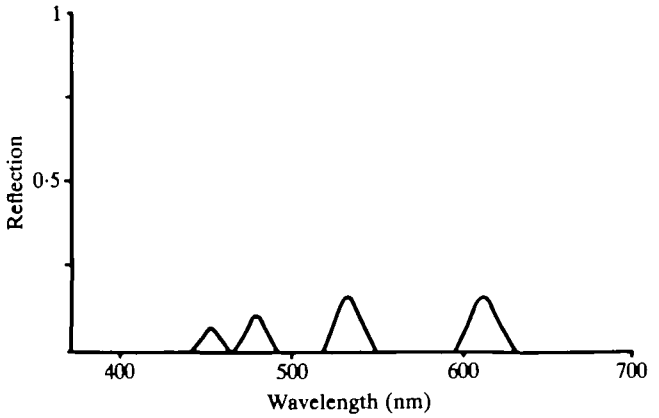

Fig. 7. Computed spectral reflectance curves for goby cornea. Values for the refractive index and thickness of the plates are shown in Table 1D. The data represent a situation where water flows equally into matrix and cytoplasm layers.

combined optical thickness of two layers, or by a change in the difference between the refractive indices of the two layers. A transfer of material between two layers involves both these changes. Two situations are envisaged in Table 1B,C and in Figs 5 and 6. The most efficient mechanism for increasing the amplitude of R_{max} without altering λ is likely to be when the movement of material causes Nb−Na to increase and the difference between Nb·Db and Na·Da to decrease. This type of situation occurs when the intercellular matrix has a low refractive index and is thin compared with the cytoplasm plates and is shown in Table 1B and Fig. 5. An optically less efficient system occurs when it is the intercellular matrix that is thin and has a higher refractive index than the cytoplasm (Table 1C; Fig. 6).

Although the wavelength of R_{max} may not change during the course of light adaptation, it does vary between sets of measurements (Fig. 3A–C). We think that this may be because the stress-related flow of material into, or out of, the iridophore controls the wavelength of reflected light, whereas it is the light-related redistribution of material within the iridophore that is responsible for the amplitude changes. Thus it is possible that the two mechanisms can act independently.

It is not easy to explain why the initial curves measured before the period of dark adaptation are lower in amplitude than those measured after a period in the light following dark adaptation. Possibly the difference in refractive indices of the two layers is reduced owing to the inflow of material into both layers. Perhaps stress, which appears to result in the red reflections from newly caught fish, causes a greater swelling in some iridophores than others, which would result in the broadening of the reflectance curve measured from several cells.

The actual values of the refractive indices of the two layers in the cornea are not known precisely enough to say which of the two layers has the highest refractive index. In the wrasse *Crenilabrus melops* (which does not appear to have a light-

induced colour change), the material of the matrix layer is continuous with the matrix separating the collagen fibrils. The matrix in the mammalian cornea stroma has a refractive index of 1·374 (Cox *et al.* 1970). Cytoplasm varies in refractive index but will not be less than 1·33 (the value quoted by Land, 1972) and is unlikely to be more than 1·56, which Land quotes as the value for proteins such as collagen or keratin. We have little reliable information about the thickness of either layer because electron microscope measurements are so unreliable (see Lythgoe, 1975; Lythgoe & Shand, 1982, for discussions). In neon tetra iridophores the presence of guanine–hypoxanthine plates makes it certain that these are thinner and have a higher refractive index than the cytoplasm. It is also unlikely that they change in either refractive index or thickness; we can thus be fairly sure that light causes an inflow of material, perhaps water, into the cytoplasm of the iridophore. In goby cornea we can be fairly certain that an important part of the light-induced colour change comes from the transfer of material between the two layers, but we cannot say in which direction the transfer takes place in response to light or darkness.

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