J. exp. Biol. (1979), 83, 249–259
With 7 figures
Printed in Great Britain

OCCLUSABLE YELLOW CORNEAS IN TETRAODONTIDAE

BY S. J. APPLEBY AND W. R. A. MUNTZ
Department of Biology, University of Stirling

(*Received* 17 *January* 1979)

SUMMARY

In three species of brackish-water puffer fish (Tetraodontidae) the corneas are colourless in the dark but become yellow in the light, through the migration of pigment in chromatophore cells lining the corneal margins. Spectrophotometry indicted the pigment to be a carotenoid. The threshold and time course of pigment migration were determined, and the effects of unilateral illumination and optic nerve section suggest that the movement is under local control. It is shown that the increase in optical sensitivity obtained by clearing the eye of pigment should be advantageous for fish living in clear water.

INTRODUCTION

Recent work by Orlov *et al.* has shown that in some species of Hexagrammid fish the cornea is deep red or yellow when the fish is in bright light, but loses colour as light intensity is lowered (Orlov, Gamburtzeva & Alexandrova, 1975; Orlov & Gamburtzeva, 1976*a*, *b*; Gamburtzeva & Orlov, 1976). The cornea of the South American puffer fish *Colomesus asellus* responds in the same way (N. A. Locket & W. R. A. Muntz, unpublished observations). It would appear that by removing the coloration these fish can increase optical sensitivity when it would be most important. Advantages of the coloration are presumably similar to those suggested to be conferred by the stable yellow pigmentation in many other teleosts (Walls & Judd, 1933; Moreland & Lythgoe, 1968; Bridges, 1969; Muntz, 1973).

The present paper reports the presence of such 'occlusable' yellow corneas in three species of brackish-water puffer fish from South-East Asia, investigates the control of pigment movement, and considers the adaptive significance.

METHODS AND RESULTS

I. *Material*

Fish were obtained from local dealers, and identified by the British Museum (Natural History). (Specimens have been incorporated into the BMNH collection with the following registered numbers. *Tetraodon steindachneri*, 1978.4.22:1. 1978.4.22:3, and 1978.4.22:4. *Sphaeroides lunaris*, 1978.4.22:2. *Tetraodon*

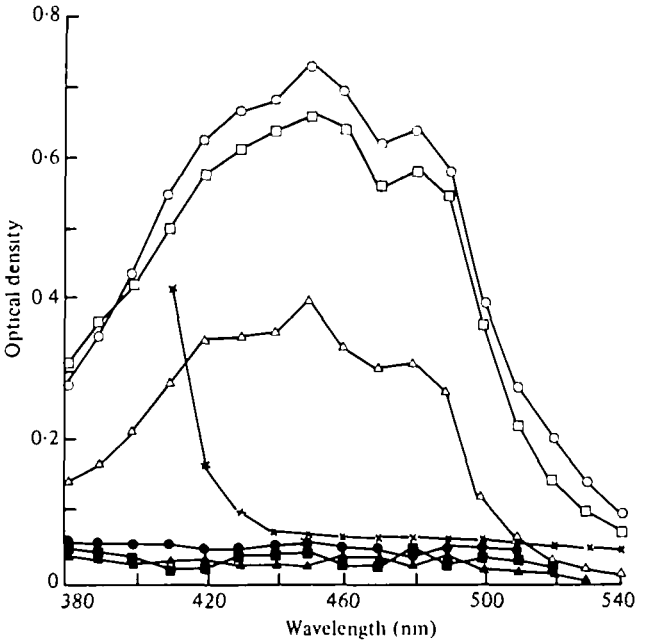

Fig. 1. The spectral absorbance of corneas from light- and dark-adapted puffer fish. The empty symbols show results for light-adapted specimens of *Tetraodon steindachneri* (circles), *T. nigroviridis* (squares), and *Sphaeroides lunaris* (triangles). The filled symbols show the results for dark-adapted specimens of the same three species. The spectral absorbance of the lens of *T. steindachneri* is also shown by the crosses.

nigroviridis, 1978.4.22.5.) Spectrophotometry was carried out on specimens of *Tetraodon steindachneri* Dekkers, 1975, *T. nigroviridis* Marion de Proce, 1822, and a lagocephalid, probably a juvenile *Sphaeroides lunaris* (Bloch). The remaining experiments were all done on specimens of *T. steindachneri*. All stock fish were kept in 50% sea water at a temperature of 23 °C, and illuminated for 12 h per 24 h cycle. The stock tanks were of glass resting on white polystyrene, and when the lights were on the luminance of the bottom of the tank, measured with an SEI photometer, was approximately 1·8 log millilamberts.

II. *Spectrophotometry*

(A) *Intact corneas and lenses*

Spectral absorbance through the centre of corneas taken from all species, and the lens of *T. steindachneri*, were measured using the spectral spectrophotometer described by Muntz (1973, 1976*b*), which has a rectangular measuring spot 0·1 × 0·8 mm. Light-adapted fish were taken from the stock tank; dark-adapted fish were adapted for 3 h. The fish were killed by decapitation, the eyes removed, and the corneas separated and placed on a glass slide under glycerol. For dark-adapted fish the procedures were carried out using a dim red photographic safe light.

In each species the light-adapted corneas showed an absorption peak at 450 nm. with a second absorption band at 480 nm and indications of a short wavelength shoulder at about 425 nm (Fig. 1). The maximal density of the cornea was con-

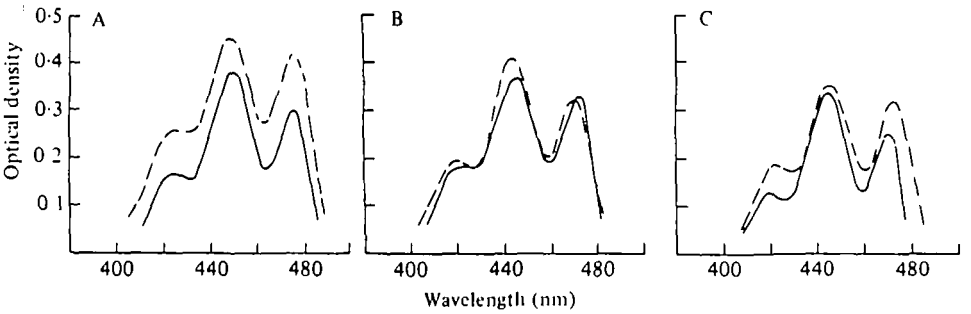

Fig. 2. Spectral absorbance of corneal and skin pigments of puffer fish, extracted in ethanol. (A) *Tetraodon steindachneri*; (B) *T. nigroviridis*; (C) *Sphaeroides lunaris*. In each case the broken line shows the results for the skin pigment, and the continuous line for the corneal pigment.

siderably less in *S. lunaris* than it was in the other two species. In dark-adapted specimens the centre of the cornea was in all cases spectrally neutral and of low optical density. The lens of *T. steindachneri* acted as a cut-off filter, and below 410 nm its density was too great (O.D. > 1·0) to measure with the apparatus.

(B) *Extracted pigment from the cornea and the skin*

Corneas from light-adapted fish were cut into small pieces, placed in 5 ml of 100% ethanol, and shaken continuously for 15 min. A piece of yellow skin from the dorsal surface of each species was also extracted in the same way. The absorption spectra of the pigment extracts were obtained using a Cecil CE 505 double-beam spectrophotometer, and are shown in Fig. 2. The pigments from the corneas and skins of the three species are all spectrophotometrically indistinguishable from each other, indicating that the same pigment is involved in each case. Three clear maxima are present: at 420, 444 and 470 nm; wavelengths a few nm shorter than those of the corresponding maxima found with intact corneas. It is known that organic solvents can bathochromatically shift the maxima of many carotenoids, including those obtained from fishes (Bridges, 1969).

III. *Time course and thresholds of the pigment migration*

(A) *Methods*

An experimental glass tank was used which was divided by a sheet of white Perspex at 135° to a horizontal light source (100 W tungsten filament bulb). The luminance from the sheet of Perspex was measured from above using an SEI photometer. The Perspex was found to reflect 87·5% of the light reflected by a standard magnesium oxide reflecting surface placed at the same angle to the light source. The luminance values in millilamberts measured with the photometer have therefore been converted into illuminations in lux falling on the fish from the light source by multiplication by a factor of 13·24. The tank and light source were contained within a light-tight black polythene enclosure. Throughout the experiments the experimental tank temperature was maintained at 23 °C.

After a given treatment a fish was killed and the corneas removed, placed on a glass slide under glycerol, and photographed with a Zeiss Tessovar photomicroscope, using a Kodak Wratten 80A filter to increase the contrast of the yellow

pigment. From these photographs (e.g. Fig. 3) tracings were made around the circumference of the whole cornea, and around the area over which the chromatophore processes contained pigment. These tracings were cut out and weighed to estimate the percentage of the cornea covered by pigment. Repeated measurements showed that only small errors result from this method: the cornea shown in Fig. 3B was, for example, measured on six separate occasions giving estimates ranging from 49·4 to 52·7%.

(B) *Time course of pigment dispersion and aggregation*

To measure the time course of pigment dispersion five fish were dark-adapted for 60 min in a light-tight tank, and then transferred to the experimental tank at an illuminance of 2·79 log lx. After periods of 5, 10, 15, 30 and 60 min a fish was killed and the extent of corneal coverage measured as described above. This experiment was repeated with a reduced illuminance of 0·79 log lx and with two extra time intervals of 2 and 4 h.

Pigment aggregation was measured by light adapting the fish at an illuminance of 2·79 log lx for 60 min and the placing them in the dark tank. A fish was removed and the corneal coverage measured after intervals of 5, 10, 15, 30 and 60 min.

The results are shown in Fig. 4. Both pigment dispersion and pigment aggregation were relatively slow, taking 60 min or more to become complete. Pigment dispersion occurred at a slower rate at lower levels of illumination, and the final level of coverage achieved was lower.

(C) *The threshold for pigment dispersion*

Individual fish were dark-adapted for 1 h and then placed in the experimental tank for 10 min at one of five illuminances, ranging from 0·09 log lx to 2·79 log lx. Following illumination the fish were killed and the degree of pigment migration determined (Fig. 5). The threshold appears to be at about 0·79 log lx, at which illuminance slow pigment migration occurred (Fig. 4). Above 1 log lx further increases in illuminance had little effect.

IV. *The locus of control of pigment migration*

Experiments were carried out to determine whether the migration of the corneal pigment was under central or local control, by studying the effects of unilateral illumination and of sectioning the optic nerve on one side.

(A) *Unilateral illumination*

A fish holder was constructed, lined with foam rubber, which held the fish loosely in position so that it could be illuminated from one side. A small black rubber cap was held lightly over the 'dark' eye by a foam-rubber pad acting against the side of the holder, and the illuminated side of the holder was covered in black polythene except for a 5 mm diameter aperture positioned over the 'light' eye. The entire holder was submerged in a glass tank at stock temperature and salinity, and water was circulated through it during the experiment. The fish was dark-adapted for 1 h before being placed in the holder, and one eye illuminated at approximately 2·79 log lx for 1 h, after which the pigment coverage of both corneas was measured.

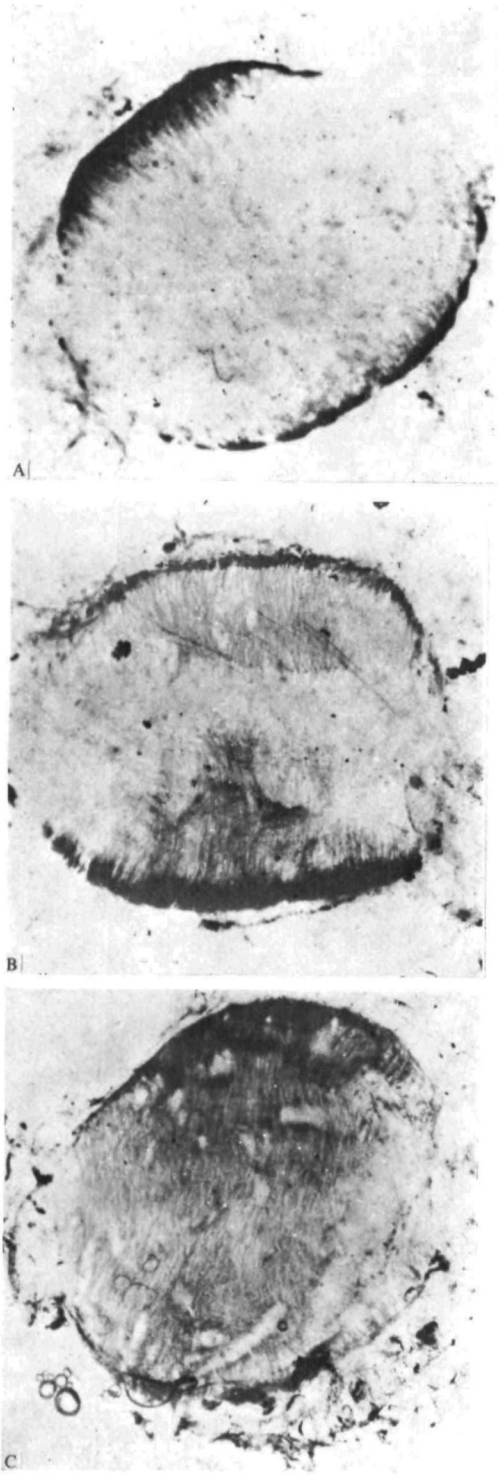

Fig. 3. Photographs of corneas from (A) dark-adapted (18% coverage), (B) partially light-adapted (10 min at 2·79 log lux, 51% coverage) and (C) light-adapted (60 min at 2·79 log lux, 92% coverage) specimens of *Tetraodon steindachneri*.

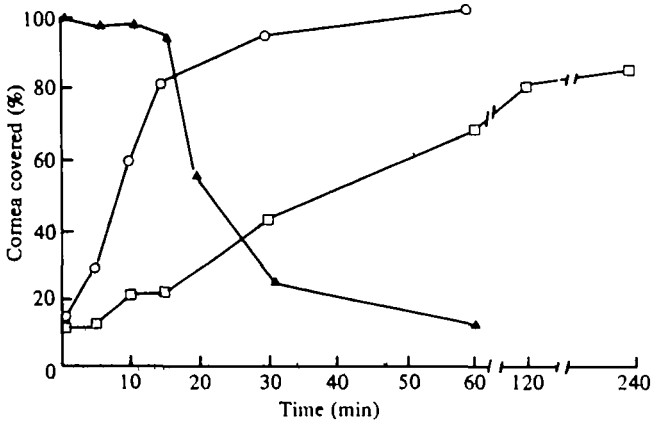

Fig. 4. The time course of pigment aggregation and dispersion in *Tetraodon steindachneri*. The empty circles and squares show the rate of dispersion for specimens exposed to 2·79 log lx and 0·79 log lx respectively; the filled triangles the rate of aggregation for fish placed in darkness.

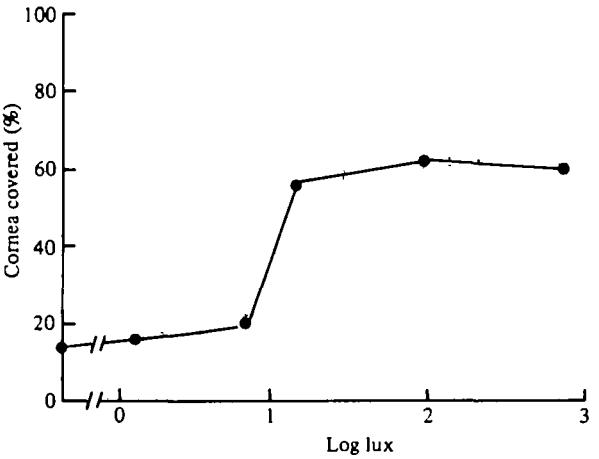

Fig. 5. The effect of different levels of illumination on the degree of pigment dispersion following an illumination period of 10 min.

In this fish, pigment dispersion was limited to the illuminated eye, in which the pigment was found to cover 100% of the corneal surface. In the 'dark' eye the pigment covered 18% of the corneal surface, which is no different from dark adapted controls.

(B) *Optic nerve section*

The optic nerve was sectioned on one side in fish anaesthetized with benzocaine, through a small incision into the orbit above the eye. Two fish were light-adapted for 2 h at 2·79 log lx before the operation, and returned to the adaptation tank for a further 6 h after the operation to recover. Following this they were placed in a dark tank for 1 h, and then killed and the corneas examined.

A third fish was dark-adapted before the operation, and returned to the dark tank for 6 h to recover. It was then light-adapted at 2·79 log lx for 1 h, killed, and the corneas examined.

Section of the optic nerve had no effect on either pigment aggregation or dispersion. In the two fish initially light-adapted and then placed in the dark, the pigment was found to cover between 14% and 18% of the cornea in both the operated and unoperated eyes, which is the coverage expected in dark-adapted fish. In the fish that received the reverse treatment the corneas of the operated and unoperated eyes both showed over 96% coverage with pigment.

DISCUSSION

The spectral absorbance curves for the intact corneas of the three species of puffer fishes used in these experiments are similar to those previously reported for the stable yellow corneas of other teleost fishes, and for the yellow corneal chromatophores of the occlusable corneas of the Hexagrammidae (see Introduction). The ethanol extracts show that the same pigment is responsible for the yellow colouration of the skin. Orlov & Gambrutzeva (1976*a*) have shown that corneal chromatophores are in several respects similar in ultrastructure to skin melanophores, with which they may share a common origin.

The characteristic three peaks of the absorption spectra indicate that the pigment is a carotenoid: the peaks of the spectra of the ethanol extracts agree, for example, with those of β-carotene dissolved in ethanol (Vetter *et al.* 1971). A definite identification is not possible on the basis of the present absorption spectra, but it is clear that this carotenoid, which Walls & Judd (1933) refer to as ichthyocarotin, is widespread among fishes.

The occlusable corneas of the Tetraodontidae are clearly very similar to those of the Hexagrammidae. In both cases the cell bodies line the upper and lower edges of the cornea with processes extending vertically over the cornea surface; the time course of the movements is slow; and the speed of the movements and final level of coloration achieved depend on the level of illumination to which the animals are exposed. Orlov & Gamburtzeva (1976*b*), using methylene blue, failed to find any innervation of the chromatophore cell bodies. They have therefore suggested that the control of the movements is not through nervous mechanisms, nor through any muscular mechanism that might, for example, contract round the cell bodies forcing the pigment into the processes, but is rather due to an autonomous non-reflex servo mechanism. Orlov and Gamburtzeva also showed that the corneal chromatophores and their processes contain many microtubules, and that injection of colchicine into the ocular bulb causes the corneal response to become slower and weaker. Microtubules are known to be directly concerned with the dispersion and aggregation of pigment granules in melanophores (Murphy, 1975), and they may fulfil a similar function in corneal chromatophores.

The present experiments on unilateral illumination and optic nerve section support the idea that the corneal response is autonomous. Corneal chromatophores would thus differ from the majority of chromatophore systems, in which control is central. The observation that only the illuminated eye shows pigment migration

precludes control by a centrally released hormone such as melanophore stimulating hormone, and would also appear to rule out the involvement of the pineal (Bagnara, 1963) or any other photoreceptive organ, since the apparatus restricted the illumination to the surface of one eye. Since cutting the optic nerve of one side was without effect (both eyes showed identical responses) central nervous control is also ruled out, although it remains possible that nervous control occurs through the autonomic nervous system as in the pupil response of *Uranoscopus* (Young, 1931). The possibility that there is both a local response and central regulation is also not ruled out.

The corneal chromatophores show similarities to some of the photomechanical movements in the retinas of other fishes. Nicol (1965), for example, has shown that central nervous and hormonal mechanisms are not involved in the migration of screening pigment between the tapetal plates of *Squalis acanthias*. The rods, cones, and pigment epithelium of teleosts also show photomechanical movements, the properties of which have been reviewed in detail by Ali (1975). Such movements can occur in enculeated eyes, though they are smaller than *in vivo*, and localized illumination of the retina can cause photomechanical movements that are restricted to the illuminated area (Easter & Macy, 1978), again indicating local control. On the other hand, it has been found that following unilateral illumination the retina of the unexposed eye may not be in a perfect state of dark adaptation (Bimes *et al.* 1966), so that some nervous or humoral interaction may take place as well. It seems likely that a variety of control mechanisms exists for different species and different photomechanical movements. Whether the corneal chromatophores of Tetraodontidae are themselves photosensitive, or the retina releases some local chemical messenger, possibly into the choroidal circulation, or there is some other mechanism of control altogether, must await further experiments.

Finally, the adaptive significance of occlusable yellow corneas should be considered. The function of yellow corneas and lenses has been discussed on many occasions, and a number of plausible suggestions put forward (see, for example, Muntz, 1972, 1976*a* for reviews). Yellow filters may be effective in reducing chromatic aberration, or in reducing the effect of veiling light when this is caused by Rayleigh scattering. They may also improve the contrast of specific objects under certain conditions: it has, for example, been suggested that in clear oceanic waters such filters will render bioluminescence more conspicuous (Somiya, 1976; Muntz, 1976*c*). By having a mechanism whereby the yellow filtering pigment can be removed, one obvious disadvantage – loss of sensitivity – can be avoided.

To assess the effect upon sensitivity, the relative number of quanta absorbed by a visual pigment in the retina, in the presence and absence of a corneal yellow filter, was calculated for various depths and various water types. Since some puffer fish are known to have two visual pigments, one based on vitamin A_1 and the other on vitamin A_2 (Munz, 1958; Schwanzara, 1967), the calculations were done for VP 502_1 and VP 535_2 (terminology of Dartnall, 1962) at an assumed optical density in the retina of 0·5, which is fairly typical for fish retinas (Denton, 1959; Muntz, 1975).

At 455 nm the optical densities of light-adapted corneas of *Pleurogrammus monopterigius* and *Colomesus asellus* are 1·1 and 1·0 respectively, and the yellow component of the cornea of *Hexagrammos octogrammus* has a density of 1·4 at this wavelength

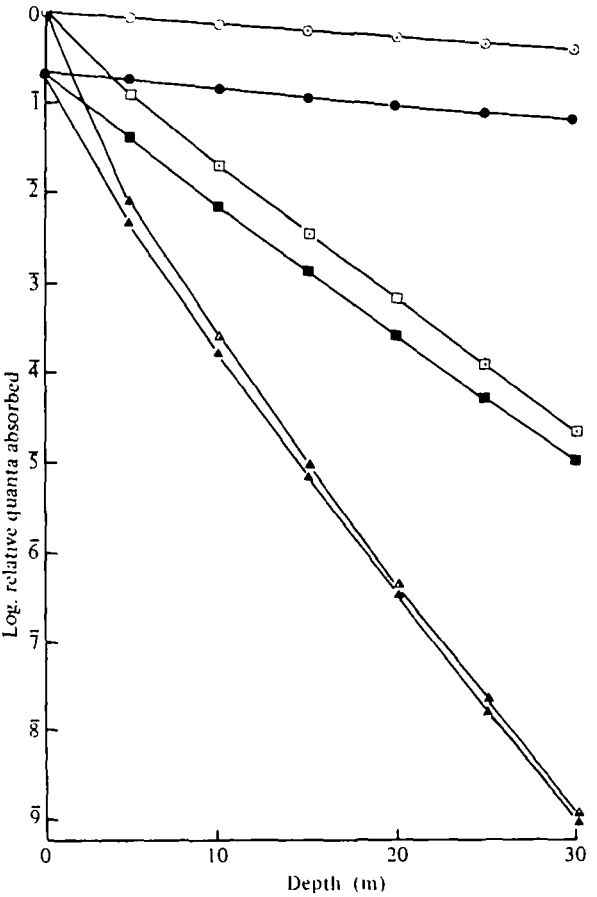

Fig. 6. Calculated number of quanta absorbed by VP 502_1 at different depths, in the presence and absence of a corneal filter, relative to the number absorbed at the surface without a filter. Empty symbols, results without a filter; filled symbols, results with filter. Circles, water type Jerlov 1 A; squares, water type Jerlov 5; triangles, water type Jerlov 9.

(Orlov & Gamburtzeva, 1976*a*; N. A. Locket & W. R. A. Muntz, unpublished observations). A corneal density of 1·4 at 455 nm was chosen for the calculations, using data of Muntz (1973) for the cornea and lens of *Astronotus ocellatus*, since using a relatively high density should emphasize any advantages of occlusable corneas. However, the corneas of the puffer fish used in the present experiments contained pigment at a lower density than this, so the calculations were also done for a cornea and lens having the characteristics shown for *T. steindachneri* in Fig. 1 (corneal density 0·73), and assuming the lens characteristics could be extrapolated linearly to shorter wavelengths.

The surface illumination was taken from the data of MacFarland & Munz (1974) for twilight at Eniwetok Atoll on 23 August 1970. Puffer fish occur in a wide variety of water types, ranging from coral seas to the highly turbid brackish waters in habited by the species used in the present study. The calculations were carried o for waters of Jerlov types 1 A, 5 and 9 (Jerlov, 1968), so as to represent a reasonable

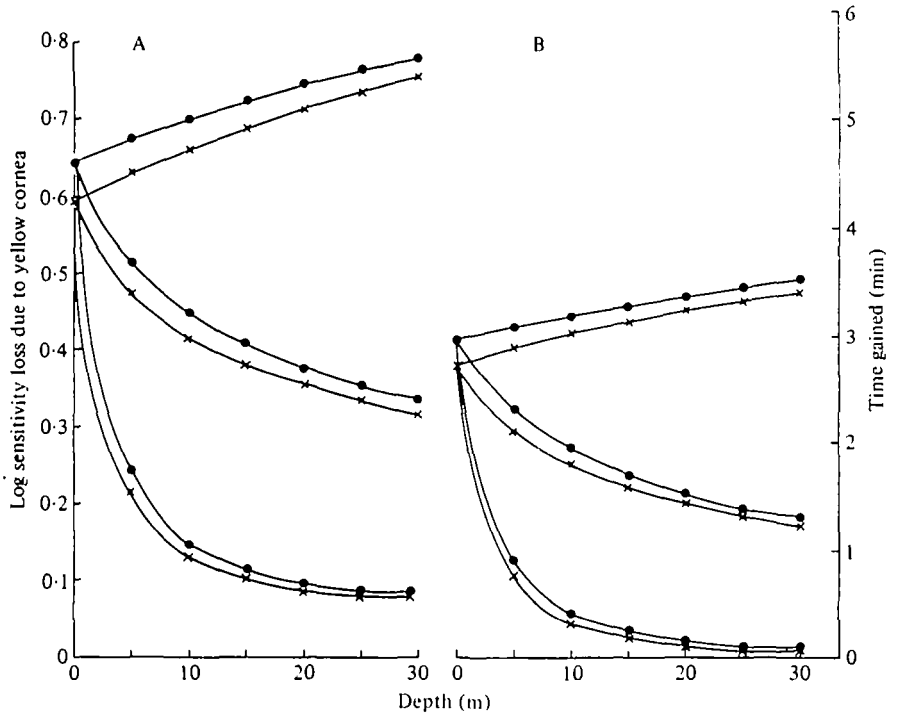

Fig. 7. Calculated effects of a yellow cornea on sensitivity for different water types and different depths. (A) Corneal density 1·4 at 455 nm. (B) corneal density 0·73 at 455 nm. For each pair of curves the dots show the results for VP 502_1 and the crosses for VP 535_2. In each part of the figure the top pair of curves is for water type Jerlov I A, the middle for Jerlov 5, and the bottom for Jerlov 9. The left-hand axis shows the sensitivity loss caused by the yellow cornea in log units. The right-hand axis shows the extra time at twilight over which retraction of the corneal pigment would make vision possible at a given level of efficiency.

spectrum of water types (although brackish water is probably even more coloured than Jerlov type 9).

Fig. 6 shows, for VP 502_1 and a corneal density of 1·4, how the relative number of quanta absorbed decreases with depth in the presence and absence of a corneal yellow filter, for the three water types. Similar sets of curves were calculated for VP 535_2 and for both pigments with a corneal density of 0·73. From these Fig. 7 was constructed, which shows the calculated sensitivity losses caused by corneal yellow pigments at different depths. In clear water (Jerlov type 1 A) sensitivity losses are high and increase with depth, reaching over 0·7 log units at 20 m when the corneal density is 1·4, and over 0·45 log units when it is 0·73. A sensitivity loss of this magnitude means that, for a given number of quanta to be absorbed by the retina (and hence a given level of visual efficiency to be achieved), a fish with a corneal density of 1·4 would have to be about 50 m shallower than one without and a fish with a corneal density of 0·73 would have to be about 30 m shallower. Under such circumstances having an occlusable yellow cornea must be a very considerable advantage over having a stable one. It is of interest that Orlov and Gamburtzeva (1976*b*) report that Hexagrammids caught during the day at 20 m or more had colourless corneas.

In Jerlov type 9 water, however, an occlusable yellow cornea confers a much smaller advantage. The sensitivity gain is greatest at the surface and decreases with depth, until at 20 m it is under 0·1 long units when the corneal density is 1·4, representing a depth gain of less than 1 m. When the corneal density is 0·78 the corresponding sensitivity gain is only 0·02 log unit, and the depth gain under 0·5 m. The difference between the two water types is due to their different spectral qualities: the light in Jerlov 1 A water is predominantly of short wavelength, and hence heavily absorbed by a yellow cornea, whereas the light in Jerlov type 9 water is of longer wavelength, and hence less affected by such a cornea.

If we take Hobson's (1972) data for the rate at which light levels change over twilight in the tropics, Fig. 7 also allows us to estimate how much later in the evening, or earlier in the morning, the sensitivity gain achieved by having an occlusable yellow cornea would allow a given level of visual efficiency to be achieved. The right hand axis in Fig. 7 shows the calculated lengths of time gained corresponding to the sensitivity gains shown on the left hand axis. The slowness of the corneal pigment movements means that at sunset an occlusable yellow cornea would confer little or no advantage, since the rate at which the pigment migrates is as slow as the rate at which the illumination decreases. At sunrise, however, in Jerlov 1 A water a given level of visual efficiency would be achieved some 5 min earlier (depending on depth) when the corneal density is 1·4, and 3 min earlier when it is 0·73. A gain of this magnitude could be a considerable advantage, since twilight in the tropics only lasts about 20 min in all and is a time during which predation in fish communities is particularly high (Hobson, 1972). In Jerlov type 9 water the gain is very much smaller, amounting to a minute or less at 10 m or deeper.

It appears therefore that the presence of an occlusable yellow cornea should confer a considerable advantage on fishes living in clear oceanic water, and a small advantage on fishes living in brackish or freshwater. It seems likely that occlusable yellow corneas arose in the Tetraodontidae during their evolution in the sea, and were retained during the invasion of freshwater because they still gave some advantage, especially at shallow depths.

We thank P. J. Whitehead for identifying the fishes, Malanie S. Johnson for writing the computer program used for the calculations, and J. H. S. Blaxter and N. A. Locket for reading and commenting on the manuscript.

REFERENCES

ALI, M. A. (1975). Retinomotor responses. In *Vision in Fishes* (ed. M. A. Ali). New York and London: Plenum Press.

BAGNARA, J. T. (1963). The pineal and the body lightening reaction of larval amphibia. *Gen. comp. Endocrinol.* **3**, 86–100.

BIMES, G., GUILHEM, A., PEYRAUD, C. & SERFATY, A. (1976). Mise en évidence d'un mécanisme humoral dans la dynamique rétinienne d'un poisson téléostéen: la carpe commune (*Cyprinus carpio* L.). *C. r. Séanc. Soc. Biol.* **160**, 2470–2473.

BRIDGES, C. D. B. (1969). Yellow corneas in fishes. *Vision Res.* **9**, 435–436.

BURNSTOCK, G. (1958). The effect of drugs on spontaneous mobility and on response to stimulation of the extrinsic nerves of the gut of a teleostean fish. *Br. J. Pharmac.* **13**, 216–226.

DARTNALL, H. J. A. (1962). The identity and distribution of visual pigments in the animal kingdom. In *The Eye*, vol. 2 (ed. H. Davson). New York and London: Academic Press.

BENTON, E. J. (1959). The contributions of the orientated photo-sensitive and other molecules to the absorption of the whole retina. *Proc. R. Soc. Lond.* B **150**, 78–94.

EASTER, S. S. & MACY, A. (1978). Local control of retinomotor activity in the fish retina. *Vision Res.* **18**, 937–942.

GAMBURTZEVA, A. G. & ORLOV, O. Y. (1976). Krasiashchie kletki rogovitsy terpuga. *Tsitologia* **18**, 676–682.

HOBSON, E. S. (1972). Activity of Hawaiian reef fishes during the evening and morning transitions between daylight and darkness. *Fish. Bull. Nat. Mar. Fish. Ser.* **70**, 715–740.

JERLOV, N. G. (1968). *Optical Oceanography*. Amsterdam, London, New York: Elsevier.

MCFARLAND, W. N. & MUNZ, F. W. (1974). The visible spectrum during twilight and its implications to vision. In *Light as an Ecological Factor*, vol. II (ed. G. C. Evans, R. Bainbridge and O. Rackham). Oxford: Blackwell.

MORELAND, J. D. & LYTHGOE, J. N. (1968). Yellow corneas in fishes. *Vision Res.* **8**, 1377–1380.

MUNTZ, W. R. A. (1972). Inert absorbing and reflecting pigments. In *Handbook of Sensory Physiology*. Vol. VII 1. *Photochemistry of Vision* (ed. H. J. A. Dartnall). Berlin, Heidelberg, New York: Springer-Verlag.

MUNTZ, W. R. A. (1973). Yellow filters and the absorption of light by the visual pigments of some Amazonian fishes. *Vision Res.* **13**, 2235–2254.

MUNTZ, W. R. (1976*a*). The visual consequences of yellow filtering pigments in the eyes of fishes occupying different habitats. In *Light as an Ecological Factor*, vol. II (ed. G. C. Evans, R. Bainbridge and O. Rackham). Oxford: Blackwell.

MUNTZ, W. R. A. (1976*b*). Visual pigments of cichlid fishes from Malawi. *Vision Res.* **16**, 897–903.

MUNTZ, W. R. A. (1976*c*). On yellow lenses in mesopelagic animals *J. mar. biol. Ass. U.K.* **56**, 963–976.

MUNZ, F. W. (1958). The photosensitive retinal pigments of fishes from relatively turbid coastal waters. *J. gen. Physiol.* **42**, 445–459.

MURPHY, D. A. (1975). The mechanism of microtubule dependent movement of the pigment granules in teleost chromatophores. In *The Biology of Cytoplasmic Microtubules* (ed. D. Soifer). *Ann. N.Y. Acad. Sci.* **253**.

NICOL, J. A. C. (1965). Migration of chorioidal tapetal pigment in the spur dog *Squalus acanthias*. *J. mar. biol. Ass. U.K.* **45**, 405–427.

ORLOV, O. Y. & GAMBURTZEVA, A. G. (1976*a*). Changeable colouration of cornea in the fish *Hexagrammos octogrammus*. *Nature, Lond.* **263**, 405–407.

ORLOV, O. Y. & GAMBURTZEVA, A. G. (1976*b*). Dinamika okraski rogovitsy terpuga. *Biofizika* **21**, 362–365.

ORLOV, O. Y., GAMBURTZEVA, A. G. & ALEXANDROVA, M. A. (1975). Izmeneniya okraski rogovitsy glaza terpuga – novoe iavlenie v zrenii ryb. *Biologischeskie issledovaniia na Dal'nem Vostoke*, pp. 117–120.

SCHWANZARA, S. A. (1967). The visual pigments of freshwater fishes. *Vision Res.* **7**, 121–148.

SOMIYA, H. (1976). Functional significance of the yellow lens in the eyes of *Argyropelecus affinis*. *Marine Biol.* **34**, 93–99.

VETTER, W., ENGLERT, G., RIGASSI, N. & SCHWEITER, U. (1971). Spectroscopic methods. In *Carotenoids* (ed. O. Isler), Basel und Stuttgart: Birkhäuser Verlag.

WALLS, G. L. & JUDD, H. D. (1933). The intra-ocular filters of vertebrates. *Brit. J. Ophthal.* **17**, 641–675, 705–725.

YOUNG, J. Z. (1931). The pupillary mechanisms of the teleostean fish *Uranoscopus scaber*. *Proc. R. Soc. Lond.* B **107**, 464–485.