

# 7

## RETINAL ADAPTATIONS TO HABITATS

The organism, a physico-chemical entity, co-exists in delicate balance with its environment. This is manifested not only by external, morphological modifications, but also by structural and physiological changes expressed at tissue and cellular levels. These changes may be divided into two categories:- the first represents a gradual process such as, for example, a unicellular organism evolving into a multicellular one (increase in efficiency); while the second represents a more rapid form of "evolution" whereby an organism adapts to its environment by modifications of pre-existing structures (adaptive radiation). With respect to vision, light (radiation) is the single-most important factor contributing to retinal changes. These changes may, in some instances be rapid enough to be manifested during the life time of the organism, although they may be temporary and revert to the original form once the stimulant is removed.

This chapter will deal with the morphological, physiological and biochemical adaptations of the retinas of vertebrates. Specifically, the emphasis will be placed on functional morphology as it best reflects retinal modifications to adaptive radiation. Although the retinas of all vertebrates will be considered, emphasis will be placed on the retinas of fishes (Super Class Pisces) because they represent nearly half of the living species of vertebrates (about 19 000 out of 40 000). In addition, fishes occupy a wide range of habitats and this diversity is reflected in the retina, of which a much greater variety has been found in fishes than any other class of vertebrates. Retinal modifications will be considered not from a taxonomic aspect, but rather from the point of view of the habitat (Fig. 7.1). In each instance the structure, visual pigment(s) and several established physiological aspects will be considered.

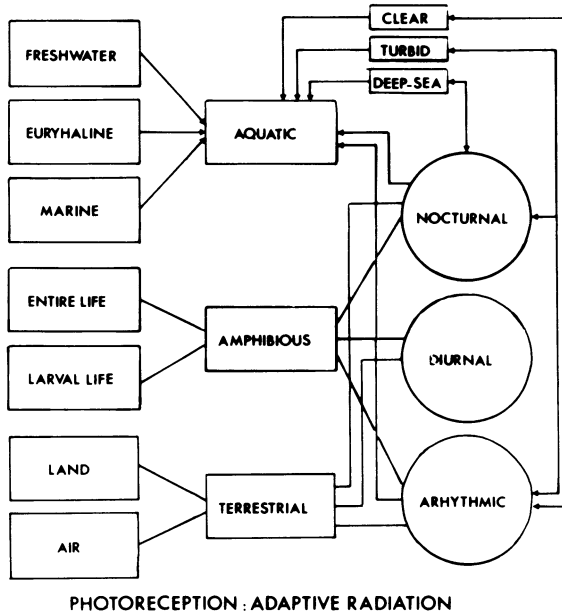


Fig. 7.1: Diagrammatic representation of the habitats and habits of vertebrates.

### Aquatic Medium

This medium may be approached from the salinity and photic aspects. Temperature also influences visual pigments and retinal functions, but it is not an adaptive force in the strictest sense and will be considered only briefly later.

There is a remarkable correlation between visual pigments and the aquatic environment. The rod visual pigment of the freshwater vertebrate is principally porphyropsin (the vitamin  $A_2$  aldehyde (retinal<sub>2</sub>), 3-dehydroretinal - based photopigment) while in the marine vertebrate it is rhodopsin (the vitamin  $A_1$  aldehyde (retinal<sub>1</sub>), retinal - based photopigment). Proponents of the theory that vertebrates originated in freshwater state that porphyropsin is the ancestral visual photopigment (Romer & Grove, 1935; Smith, 1932; Wald 1942); while opponents of this theory (Denison, 1956; Crescitelli, 1972) dispute this, and believe that rhodopsin is the ancestral visual pigment since life itself originated in the sea.

Predominance of rhodopsin/porphyropsin is apparent not only in strictly marine/freshwater fishes (Fig. 7.2), but also in migratory fishes (anadromous, catadromous). Catadromous fishes (e.g. killifish, *Fundulus heteroclitus*; eel, *Anguilla* spp.) which spawn in the sea, but mature in freshwaters show a predominance of rhodopsin while in the sea and porphyropsin while in freshwater. In contrast, anadromous fishes (e.g. white perch, *Morone americana*; the sea lamprey, *Petromyzon marinus*) spawn in freshwater, but spend their juvenile to adult life in the sea. These fishes possess both visual pigments, but exhibit a higher porphyropsin-rhodopsin ratio while in freshwater and the reverse in marine waters.

Although further studies are still necessary, it is apparent that changes in retinal photopigments accompany the metamorphic transitions during the life cycle. Many salmonid fishes perform anadromous migration too, however, the question as to whether or not a phototransition is associated with this migration has not been answered with certainty.

In addition, to the marine-freshwater migration and vice versa, a pigment shift is also manifested in the larval to adult transition of amphibians. Larval amphibians which inhabit a strictly aquatic environment have a porphyropsin rich retina. In some, on maturity, the dorsal (aquatic) retina remains rich in

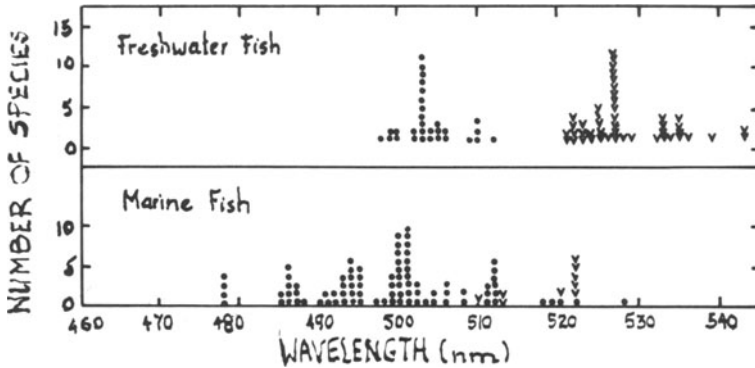


Fig. 7.2: Visual pigment distribution in marine and freshwater fishes. Each point represents the wavelength for maximal absorbance for a single species.

- -rhodopsin
  - ▼ -porphyropsin
- (After Crescitelli, 1972)

porphyropsin, while the predominant visual pigment in the ventral (aerial) retina is rhodopsin (e.g. Rana catesbeiana, Fig. 7.3). The four-eyed fish (Anableps anableps) which is also capable of both aerial and aquatic vision (Fig. 4.5) shows not only retinal, but also visual pigment distribution representative of the two media. Rhodopsin is predominant in the ventral (aerial) retina, while porphyropsin is dominant in the dorsal (aquatic) retina.

The electrical activity of photoreceptors in response to incipient light may be recorded from the horizontal cells (S-potential; L (luminosity)-response, wavelength independent; C (chromaticity)-response, wavelength dependent). Comparison of the S-potentials of marine and freshwater fishes shows that in freshwater fishes these responses are shifted towards longer wavelengths (red) while in marine fishes the shift is towards shorter

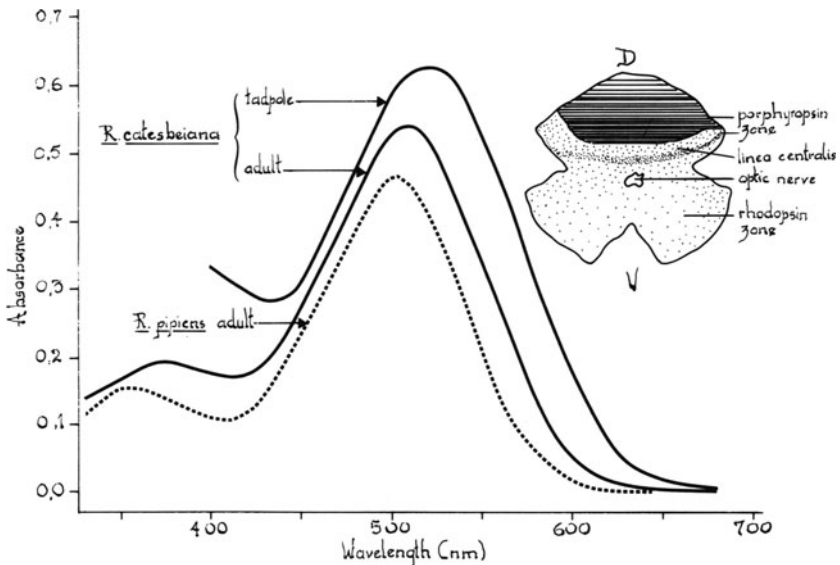


Fig. 7.3: Unbleached retinal extracts from tadpole and adult of Rana catesbeiana (solid curves) and adult of Rana pipiens (dotted curve). The extract of R. pipiens contains only rhodopsin; while the extract of R. catesbeiana, on the other hand, contains almost pure porphyropsin ( $\approx 4\%$  rhodopsin). Adult R. catesbeiana, on the other hand, contains both rhodopsin and porphyropsin.

-see inset for the distribution of these rod visual pigments in the dark-adapted R. catesbeiana retina.

(After Reuter et al., 1971)

wavelengths (blue). In addition, spectral sensitivity curves, obtained by electroretinography (ERG), may be related to salinity. In general, the maximum peak of these curves is related to the type of rod visual pigment. Thus, in freshwater fishes the peak is at 525 nm or 530 nm, while in marine fishes it is around 500 nm. In migratory fishes or fishes from estuarine waters the peak is intermediary. Some workers in this field put forward the hypothesis that the spectral qualities of fresh and marine waters have contributed to the different spectral properties of the retinas of the fishes in these waters. However, this is not easily explainable, except that oceanic waters show less spectral variation. It is rather more probable that the differences in the spectral properties of the retinas may have resulted from other factors (availability of carotenoids, genetic factors) influencing the choice between the vitamin A<sub>1</sub>- and vitamin A<sub>2</sub>-based visual pigments.

### Photic Qualities

Studies relating retinal adaptations (morphological, biochemical and physiological) to photic conditions have proven more fruitful. Organisms inhabiting the aquatic environment are exposed to a wide range of photic conditions, much more so than those in the terrestrial environment, and excellent correlations have been established between the functional retinal structure and the environment.

### Clear Waters

Light can penetrate to great depths (1 000 metres) in clear waters (Fig. 7.4), however, the spectrum varies with depth (Fig. 7.5) and transparency (Fig. 7.6).

Fishes inhabiting clear, surface waters (e.g. salmon, trout) tend to have large, well-developed eyes with retinas rich in both photoreceptors (rods and cones), and well differentiated inner layers (Fig. 7.7). The retina is arhythmic, and capable of functioning in a variety of light intensities. Furthermore, the retina is capable of photomechanical changes - photoreceptors and pigment granules of pigment epithelial cells are capable of reacting to the different light intensities (see Chapter 5).

The absorption spectrum of the scotopic visual pigments of fishes dwelling in clear waters shows a maximum at 500 nm for marine fishes and 525 nm for freshwater fishes; exceptions to this are the anadromous, catadromous and other fishes mentioned in the section above (Aquatic Medium). With decreasing transparency,

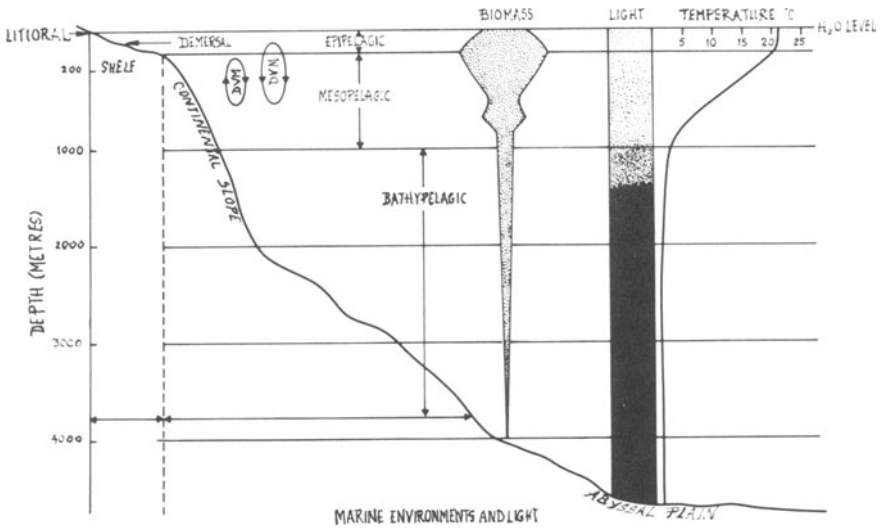


Fig. 7.4: Diagrammatic representation of the relationships between the penetration of light, temperature and biomass at different oceanic depths. The gradient of the ocean bed is exaggerated.

**DVM** - diurnal vertical migration.  
(After Marshall, 1971)

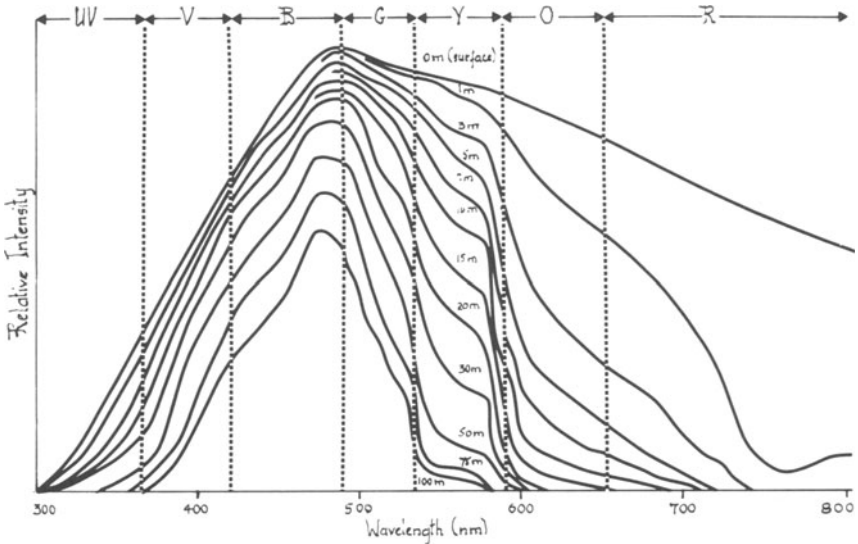


Fig. 7.5: The spectral distribution of solar energy after

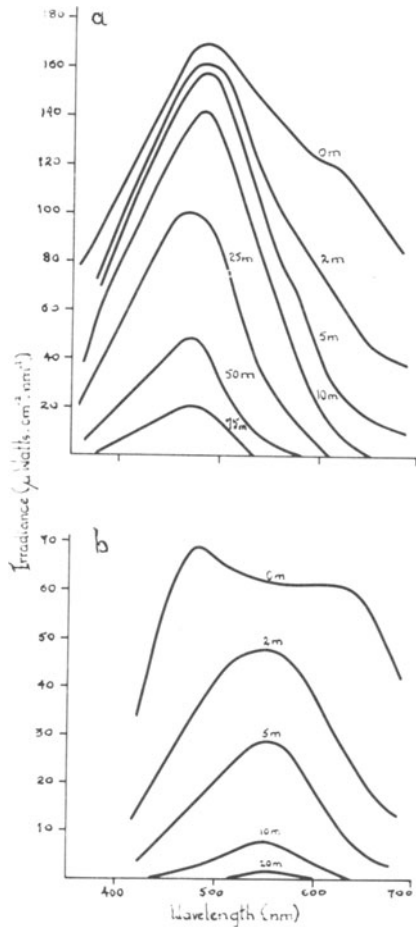


Fig. 7.6: Spectral distribution curves for clear ocean water (east Mediterranean Sea; **a**); peak in blue light ( $\approx 470$  nm) and the ultraviolet is strong even at great depths. An entirely different situation exists in the Northern Baltic Sea (**b**). The presence of particulate matter and yellow substances shift the maximum transmittance towards 550 nm; ultraviolet is rapidly extinguished in the surface stratum. (After Jerlov, 1970)

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passing through successive depths of distilled water. Note that red and orange radiations are absorbed most strongly while the least affected wavelengths are in the blue. (After Clarke, 1939)

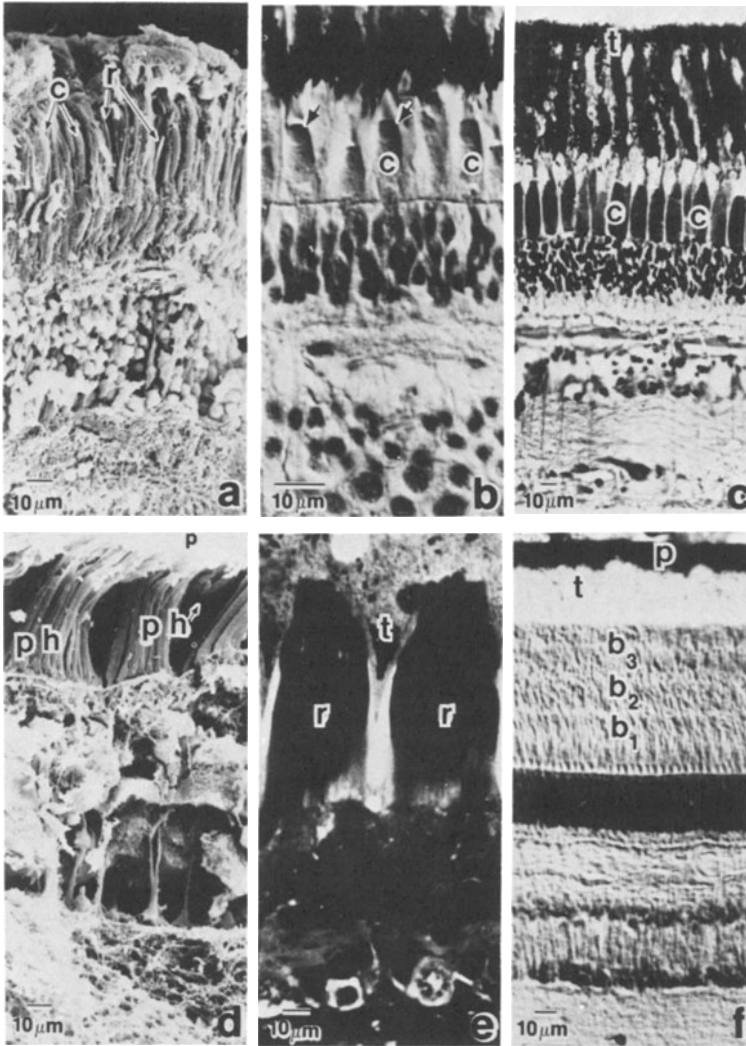


Fig. 7.7.: Photomicrographs (b, c, e, f) and scanning electron micrographs (a, d) of the retinas of fishes inhabiting different habitats.

a - the duplex retina of the brook trout (*Salvelinus fontinalis*) which lives in clear waters; b - the retina of the killifish (*Fundulus heteroclitus*) which lives in slightly turbid and green-hued waters, note the oil droplets (arrows); c - retina of the walleye (*Stizostedion vitreum*) which inhabits turbid waters, note the hypertrophic cones and the tapetum lucidum (t); d -



the absorption maximum of the rod visual pigment, whether it be rhodopsin or porphyropsin, shifts to longer wavelengths. This is true for both marine and freshwater fishes.

A similar distinction is observed in the measurements of spectral sensitivity of marine and freshwater fishes. Flicker fusion frequency (FFF) is much higher in fishes inhabiting clear waters than those in turbid waters. An excellent correlation was established between maximum FFF, the latency and components of the ERG, and the habitat and mode of life of fishes (Fig. 7.8). It is apparent that well-developed inner cellular layers and FFF are influenced by habitat. In other words, the more developed the inner cellular layers, the higher the maximum FFF; and this denotes active fishes living in clear waters. Furthermore, the well-developed inner layers, in relation to the great number of slender cones, suggest that acuity of these animals is high. Thus, the interrelation of cones and horizontal cells may also indicate the habitat and mode of life of fishes.

### Turbid Waters

Turbidity of water and air is of different degrees and types. Fig. 7.9) shows the transmission curves (at a 1 metre depth) in oceanic and coastal waters due to turbidity. From the curves it is evident that oceanic waters show less variation than coastal waters. The latter being more under the influence of the type of bed (silt, sand, mud, etc.), turbulence caused by tides, strong currents and surfs, particularly when blown by strong winds. The same range of turbidity may also be found in freshwaters. These waters may be crystal clear (e.g. Lake Malawi in Africa, Crater

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duplex retina of the mooneye (Hiodon tergisus) which also inhabits turbid waters has grouped photoreceptors (**ph**) (bundles containing both rods and cones) and a tapetum; **e** - retina of Scopelarchus guentheri which is a deep sea fish in which the rods of the pure rod retina are grouped into bundles which then act as macroreceptors; **f** - the pure rod retina of Argentina silus, another deep sea fish, here the rods are slender and are arranged into banks (**b<sub>1</sub>**, **b<sub>2</sub>**, **b<sub>3</sub>**), the pigment epithelium does not exhibit retinomotor movements and the tapetum (**t**) is well developed.

**c** - cones; **r** - rods; **ph** - photoreceptors; **p** - pigment; **t** - tapetum.

(From Ali, 1981)

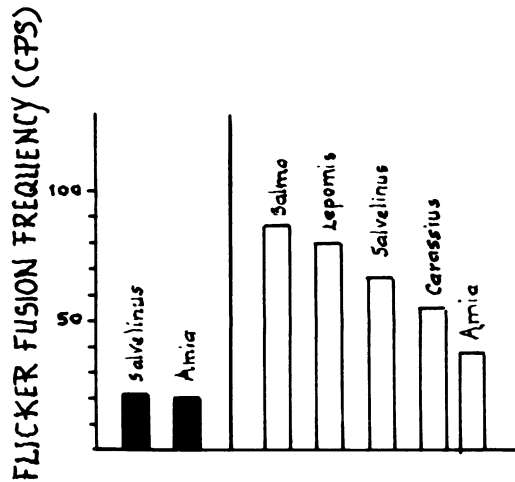


Fig. 7.8: The maximum flicker fusion frequency of the ERG of various fishes in light and darkness. The results were obtained from the same laboratory using similar techniques. Solid bars represent results from dark-adapted samples, and the clear bars from light-adapted samples. (After Gramoni & Ali, 1970)

Lake in California) on the one hand, or extremely turbid (e.g. Solimões River in South America) on the other. Between these two extremes a gradient of turbidity may be found. In addition, the waters may also be tinted, for example, by algae, dissolved materials, organic materials in suspension; while red-hued waters is usually the result of the proliferation of plankton or bacteria. Furthermore, freshwaters may show a range of pH (from acid to basic).

Studies on the retinal adaptations of fishes living in turbid waters have been approached from the point of the visual pigments, retinal structure and physiology. Retinas of fishes in turbid waters (Fig. 7.7) usually contain a high number of slender rods and few cones, the latter may be enlarged and contain inclusions (e.g. walleye, *Stizostedion* spp.) or they may be grouped (e.g. goldeye, *Hiodon* spp.). In the Hiodontidae, the rods are also grouped with the cones. Droplets or inclusions, the result of hypertrophy of mitochondria, are also observed in the killifish (*Fundulus*) which inhabits green-hued waters. Further retinal adaptations include the presence of reflecting material in the pigment epithelial cells

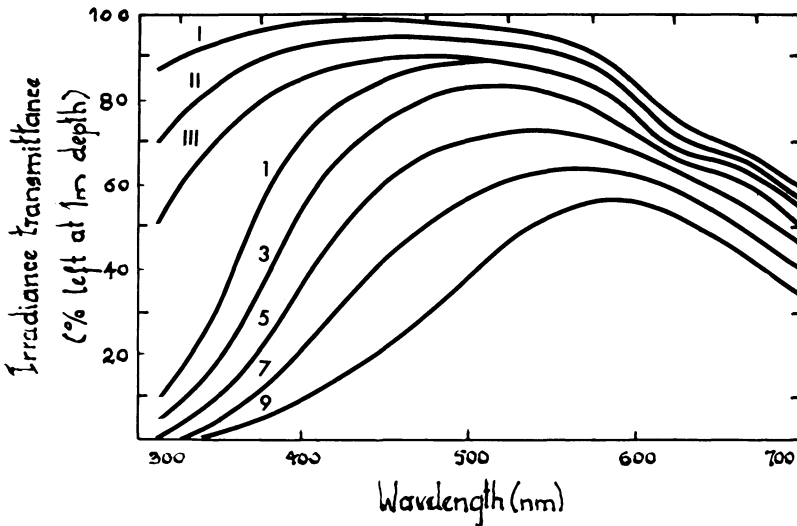


Fig. 7.9: Spectral transmittance of the three basic oceanic water types (I, II, III) and five coastal types (1, 3, 5, 7, 9) for high solar altitudes (areas off Scandinavia and northwestern USA). Note that for the two groups of curves the decrease in transmittance from one type to the next (with increasing numerical value) is most marked in short wave light. This results in a shift from a maximum transmittance from blue, in the clearest waters, over green to brown in the most turbid waters.

(After Jerlov, 1970)

(tapetum). These modifications of retinal structure are thought to be means of increasing visual sensitivity by;- increasing the number of scotopic photoreceptors (rods); converging the incipient light; and increasing the possibility of photon capture by redirecting light entering the retina twice over the outer segments of the photoreceptors. The walleye and goldeye clearly illustrate two morphological modifications employed to solve the same problem (convergent evolution).

An interesting correlation has also been established between visual pigments (rods and cones) and photic conditions. In general, the maxima of the absorption spectra of scotopic visual pigments correspond to the maxima of the transmission spectrum of the water. Thus, the more turbid the water the greater is the shift of the absorption spectrum of the scotopic visual pigment to longer

wavelengths (Fig. 7.10). This is clearly illustrated in the comparative study conducted by Pothier and Ali (1978) on three percids. With respect to the photopic visual pigments (cones), most turbid water fishes lack blue cones which to all intent and purposes are practically useless if the cornea or crystalline lens is yellow. There is another interesting point, the cichlid (Nannacara anomala) which inhabits partially turbid waters lacks green cones, but the rods are large and function both in scotopic and photopic vision as evident from the display of the synaptic ribbons (Ali et al., 1978).

At the physiological level, the ERGs latency (waves a, b, and d) are longer, and the FFF of the ERGs lower in fishes of turbid waters. It is also interesting to note that in fishes such as the walleye (Stizostedion) the maximum FFF is attained at light

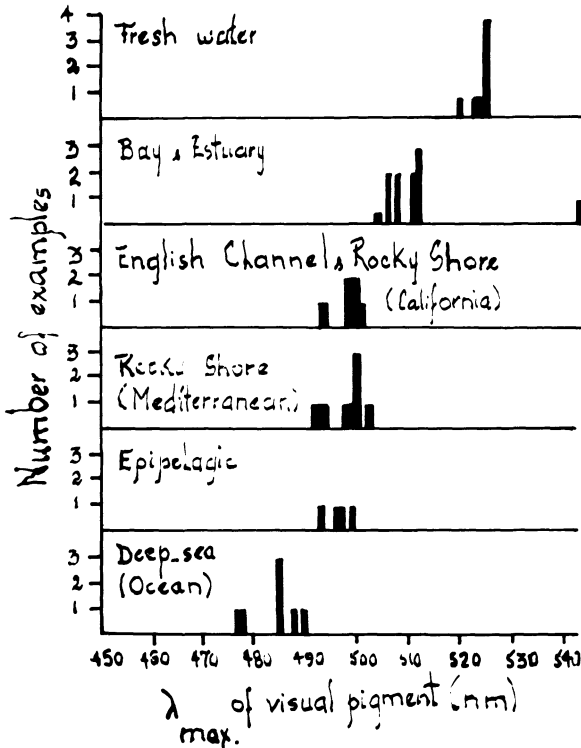


Fig. 7.10: The λ<sub>max</sub> of visual pigments extracted from eyes of fishes caught in various types of natural waters. (After Lythgoe, 1972)

intensities lower than the threshold intensities necessary to induce the dark-adapted state in the retina of fishes which possess the reflecting material (retinal tapetum) (Ali & Anctil, 1977). From this it is apparent that eyes with reflecting material utilise to the fullest the available downwelling light. In the light-adapted state, on the other hand, the reflecting material is shrouded by the melanin pigments of the retinal epithelial cells and thus there is no difference in the FFF or its maximum of light-adapted fishes containing or not containing reflecting material.

The S-potential of turbid water fishes is also different from that of clear water fishes. The peak of the L-potential is displaced to the red region, while the C-potential, which is bimodal, changes such that the sensitivity in the red is less than the sensitivity in the blue.

### Deep Sea

Even in very clear waters light does not penetrate more than 1 000 metres (Figs. 7.4, 7.6). Fishes in these waters may show not only a reduction in the function of the eye, but also in the size of the eye itself. On the other hand, the eye may be enlarged to permit structural modifications of optical structures such as the crystalline lens and cornea (see Fig. 6.9c) as well as the retina (Fig. 7.7f). Measurements of the attenuation of light as one descends show that after a depth of 500 metres only the blue-green light remains. In deeper waters there is barely any light (Fig. 7.4), and vision at these depths is tuned to bioluminescence (inter- and intra-specific). Under these light conditions retinal sensitivity is the key. Thus, cones are superfluous as photopic vision is practically non-existent; instead, rods are modified to augment sensitivity (Fig. 7.7f). The number of rods is increased, these rods are usually slender and arranged in banks; or the rods may have exceptionally long outer segments. These modifications are thought to increase the probability of photon capture by increasing the amount of scotopic visual pigment. In these fishes, photoreceptors may occupy up to 90% of the volume of the retina. Recently, however, a study on the conger eel, which has a banked retina, showed that only the vitread-most layer of rods function in photoreception while the rest were suggested to function as visual pigment reserves (Shapley & Gordon, 1980). No tangible proof was forwarded to substantiate the latter claim. In other instances, the rods may be grouped as in the Hiodon. In this fish the cones are also grouped within the rod bundles (Wagner & Ali, 1978). The inner neural layers of the retina of these fishes are not as well

developed, thus reflecting the importance accorded to summation (high sensitivity).

Scotopic visual pigments of fishes inhabiting deep waters are more sensitive to blue light, with the maximum around 480 nm. The maximum absorption spectra of almost all species of deep sea fishes studied do not surpass 500 nm. Although the spectral quality of light reaching a fish has an influence on the spectral characteristics of visual pigments it is possible to find fishes in which the visual pigments differ from the qualities of the ambient light. Nevertheless, these fishes are still well adapted according to the sensitivity hypothesis. Certain fishes (e.g. *Pachystomias*, a pelagic fish (Denton et al., 1970); *Aristostomias scintillans* (O'Day & Fernandez, 1974) a bioluminescent deep sea fish) which have photophores emitting red light also have red sensitive photopigments in the retina (See also Somiya, 1979).

The physiological studies of the retina of deep sea fishes present certain technical difficulties arising from their capture and maintenance in captivity under conditions representative of the deep sea environment. Furthermore, these fishes tend to be bloated when brought to the surface because of the rapid reduction in pressure which causes an enlargement (and even bursting) of the swim bladder.

### Tide Pools

There appears to be only one documented account of vision in tide pool fishes (Wagner et al., 1976). Ten species from as many families were studied. They may be classified as permanent dwellers and temporary dwellers. The latter group is composed of juvenile which profit from the protection afforded by this environment. However, when they mature they abandon this habitat. The typical inhabitants of tide pools may either be active forms which fully exploit their visual capacities, or bottom living forms, or hiding forms.

Based on the observations of the retinal structure of the ten fishes it is apparent that their retinal adaptations may be divided into three broad categories:- (i) fishes dependent on vision (good acuity and sensitivity); (ii) fishes specialised for vision in murky waters or dim light environment (poor acuity and/or high sensitivity); and (iii) fishes with poor visual capacity (very reduced acuity and sensitivity). In the first group the retinas are characterised by regular cone mosaics, high receptor densities and a low degree of summation. At the other extreme, in the third group, the retinal pigment epithelium is sparse, receptor density

low, summation high and integration rates low. Due to the intermediate nature of the second group, the retinal adaptations are heterogenous. The common features are low cone densities, high rates of summation and high degrees of integration. These may be coupled to specialised features; for example, Labrisomus nuchipinnis has a reduced retinal pigment epithelium, a well-developed reflecting layer, conspicuous oil-droplets and prominent grouped rods (Wagner et al., 1976). Although these features are present in the other members of the group, they are less pronounced.

### Marshes

Marshes are excellent nurseries for fishes. Evidently the presence of young fishes would attract predators, however the young predominate. Most of the species of fishes occupying this habitat abandon it when mature, but there are also those which spend their entire lives in the marshes. In general, the waters of marshes are dimly lit due to the abundance of vegetation, in addition the water may also be turbid. Thus, the retinal adaptations of fishes in marshes resemble closely that of fishes found in turbid and murky waters (Menezes et al., 1981).

### Terrestrial Environment

Retinal adaptations in terrestrial vertebrates (including aerial and burrowing vertebrates) are related to their habits rather than their habitats (adaptations to habits were considered in Chapter 6). It is interesting to note, in passing, the remarkable similarities between the retinal structure of terrestrial vertebrates which occupy different habitats but observe the same habits. For example, nocturnal animals of different habitats (such as the mouse, bat and owl) have remarkably similar retinal structure; rather, ocular adaptations are of the essence. The uniformity of retinal composition of terrestrial vertebrates also extends to the visual pigments. Spectral distribution of the sun's energy shows a broad maximum centred at 500 nm (Fig. 5.1) and it is not surprising that the majority of terrestrial vertebrates possess pigments with  $\lambda_{\max}$  within the 493 nm to 502 nm range. The reason for this is that except under dense foliage, radiation reaching the earth's surface is modified only by atmospheric absorption. Although this may vary somewhat from location to location it has a negligible effect on the spectral energy distribution, therefore negating the need for variation in visual pigments. The strictly terrestrial vertebrates will be considered here. They will be grouped into the

predator group and into burrowing and aerial animals.

Birds will be taken to represent the predator group. Almost all predator birds (except the owl) are diurnal in their habits. Four striking retinal adaptations observed in diurnal birds are:- (i) the presence of oil-droplets in the cones (these are thought to function as filters, enhancing acuity and reducing aberration); (ii) the ability of both the cones and the retinal pigment to exhibit photo-mechanical responses, the latter method of responding to light of different intensities is usually attributed to the lower vertebrates, however birds have maintained this capacity although they also exhibit pupillary changes (iris response); (iii) the presence of two foveas in birds of prey (e.g. falcon), one for binocular vision and the other for monocular vision, the foveas are also thought to enhance visual acuity; and (iv) the FFF in these birds is also very high.

The eye of burrowing animals is generally small, and the retina resembles that of nocturnal vertebrates - the majority of the photoreceptors are rods; the pigment epithelium is reduced or without pigment granules; and photomechanical movements of the photoreceptors are absent. In other words, it is a retina specialised for vision at low light intensities (high sensitivity).

The third group is composed of tree dwellers such as lizards, squirrels and monkeys; birds too may be included within this group. In this group of vertebrates the retina is adapted for high acuity - high density of cones, low degree of summation, presence of a fovea, and colour vision. Note, however, that colour vision is not limited to this group; birds of prey, fishes, etc., also possess colour vision. Some of the tree dwellers (e.g. monkey) are arrhythmic in the sense that they can see in varying light intensities - both at dawn and at dusk. These vertebrates have duplex retinas, rich in both scotopic (rod) and photopic (cone) photoreceptors. These characteristics and aptitudes are carried over to the anthropoids, some of whom are no longer tree dwellers.

### Temperature

Temperature is not a factor affecting photoreception in the strictest sense; except that like all other processes (whether they may be morphological, chemical or physiological), there is an upper and lower limit between which the process can occur. Thus, the vision of poikilotherms will come more under the influence of temperature than that of homeotherms. In the foregoing habitats discussed temperature may differ within the habitats. For



example, turbid waters may be both cold (temperate regions) or warm (tropical regions); the same holds true for clear waters and terrestrial habitats. The only habitat where there is little variation in temperature is within great oceanic depths.

Generally, in a colder environment (particularly true for poikilotherms) the primary visual process is slowed down. Consequently, the threshold is increased; while acuity and the ability to perceive movement is reduced (see Ali, 1975, for review). Furthermore, temperature has been reported to modify spectral sensitivity (Tsin & Beatty, 1977). Changes in the amount of visual pigments as well as the proportion of photopigments in species with paired photopigments are also affected by temperature. In the latter, higher temperature increases the proportion of rhodopsin, whereas lower temperature builds up the proportion of porphyropsin (see Allen et al., 1982; Tsin & Beatty, 1977). The changes in visual pigment levels is associated with the change in rod dimension (e.g. length). The increase in visual pigment levels during winter has been demonstrated in some species (e.g. trout, shiner), and it has been suggested that this leads to greater sensitivity during the dawn and dusk periods; while the increase in the ratio of porphyropsin to rhodopsin leads to sensitivity in the longer wavelengths (Allen et al., 1982). In support of this, changes in visual pigments have been correlated with appropriate changes in visual threshold in the amphibian Xenopus and albino rat (see Allen et al., 1982).

Temperature was also found to affect photomechanical or retinomotor responses, however, this was evident only in dark-adapted animals. At both ends of the temperature scale (0 - 14°C, 19 - 33°C), for frog, pigment granules of the retinal pigment epithelium migrated into the apical processes (i.e. appeared as in the light-adapted state) whereas between 14 - 18°C there was minimal expansion (i.e. as in the normal dark-adapted state). Cones too contracted in darkness at temperatures between 30 - 36°C while 3°C and 16°C had no effect. Rods appeared, relatively, unaffected (see Ali, 1975). The rate of adaptation is also affected by temperature; rate of dark-adaptation for cones and retinal pigment epithelium being extremely slow at low temperatures. Temperature, however, is not a permanent factor affecting retinal structure, rather, photic conditions is one of the chief determining factors.

### Summary

In summary, it can be said that there is an excellent correlation between the aquatic habitats and the structure and function of the retinas of fishes; and that retinal structure of terrestrial vertebrates is more uniform and reflects their habits rather than their habitats.

It is, however, important to note that other biological parameters besides the habitats must be considered when studying retinal structure and vision. More detailed studies are required to better understand retinal adaptations to the various habitats. These include:- synaptic relations, visual pigments, visual acuity, and the effect of coloured (generally yellow) cornea, oil-droplets and crystalline lens related to the functions of the retina under normal conditions or at threshold light intensities.