

'stay', and 'leave' decisions to high probability, so that, as the number of fish reduced, schools would shrink. However, schools might stay close together so that members could reassemble with their former schoolmates. Under this regime, fragility and rebuilding time would be intermediate. Measurements of the mesoscale distributions of fish shoals can distinguish among the hypotheses above. One attempt at measuring the patchy ocean distribution of herring schools is shown in **Figure 9**.

See also

Fish Feeding and Foraging. Fish Locomotion. Fish Predation and Mortality. Fisheries Overview. Mesopelagic Fishes.

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FISH VISION

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Introduction

The eyes of all vertebrates are built to a common plan, with a single optical system focusing radiation on a light-sensitive retina lining the posterior part of

the eye (**Figure 1**). It is, none the less, impossible to describe a general fish eye. Fish inhabit almost every conceivable optical environment, from the deep sea where darkness is punctuated only by brief bioluminescent flashes to the sunlit surface waters, from the red peat lochs of Scotland to the green coastal waters of the English channel and the blue waters of a tropical lagoon (**Figure 2**). Fish therefore live at all levels of illumination and are exposed to many different spectral environments. The fish

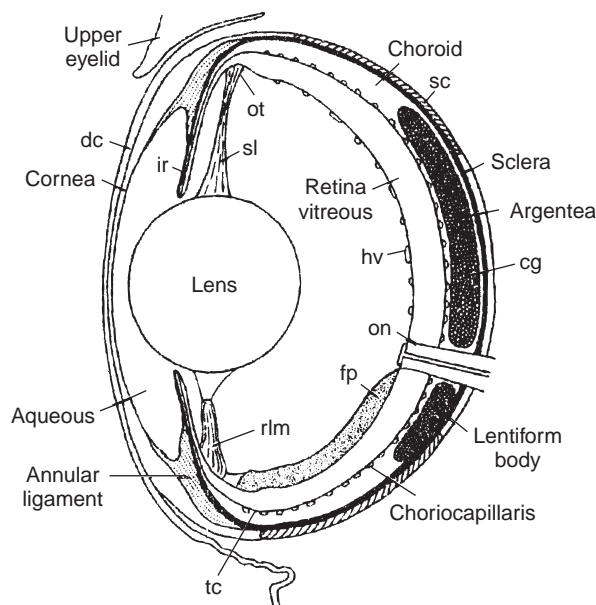


Figure 1 Schematic representation of a vertical median section through a teleost eye: cg = choroid gland; dc = dermal component of cornea; fp = falciform process; hv = hyaloid vessel; ir = iris; on = optic nerve; ot = ora terminalis; rlm = retractor lentis muscle; sc = scleral cartilage; sl = suspensory ligament; tc = position of tensor choroidea. (From Nicol (1989).)

visual system has adapted superbly to these various conditions.

Image Formation

Although most fish eyes are approximately symmetrical, with spherical lenses (Figure 1), there are several exceptions. Some bottom-dwelling flatfish and rays, for instance, have an asymmetrical eye so that the retina is at varying distances behind the lens (Figure 3). This so called 'ramp retina' results in objects at different distances appearing in focus at different points on the retina. Odd-shaped eyes are also observed in some deep-sea species. Since the last vestiges of sunlight come from above the animal, their eyes are often positioned on the top of their head. In order to accommodate as large an eye as possible – to maximize sensitivity – within a head of reasonable size, the sides of a normal eye have been removed during the course of evolution, resulting in a tubular-shaped, upward-pointing, eye (Figures 4 and 8B–D).

While in terrestrial vertebrates the major refractive surface of the eye is the cornea, the lens serving primarily to adjust the focus, in aquatic animals the only important refractive element in most fish is the lens because the similarity of the refractive indices of water, cornea, and aqueous humor neutralize the optical power of the cornea. Thus, while the lenses

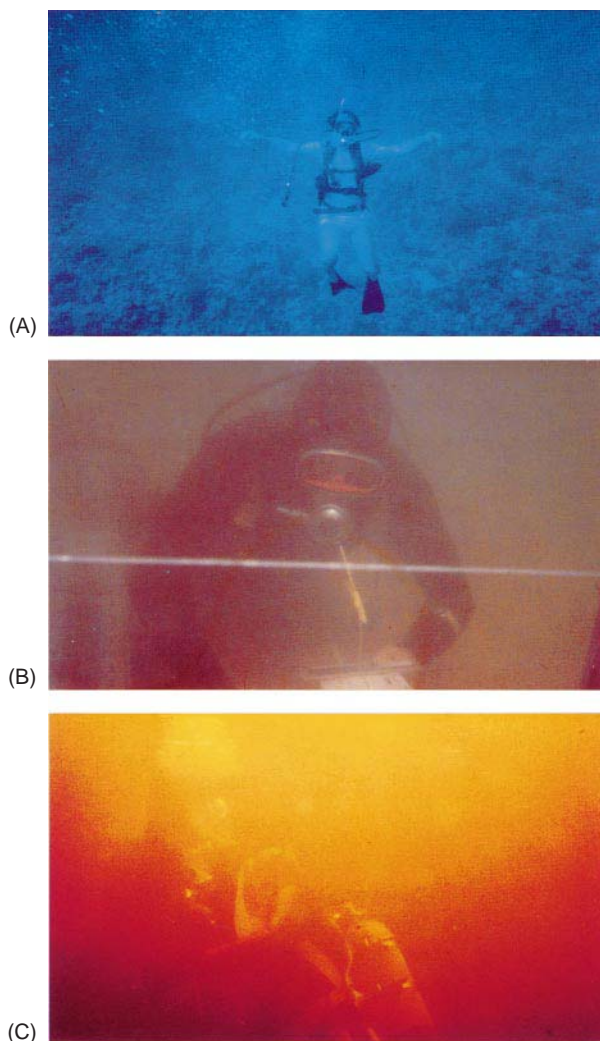


Figure 2 The author in three different bodies of water, illustrating the diversity of the underwater light environment: (A) Cayman Islands; (B) English Channel; (C) Loch Turret (Scotland).

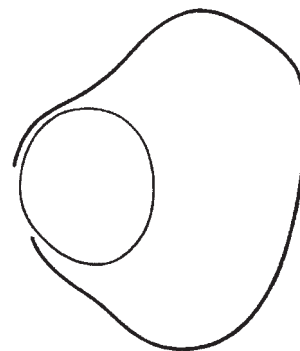
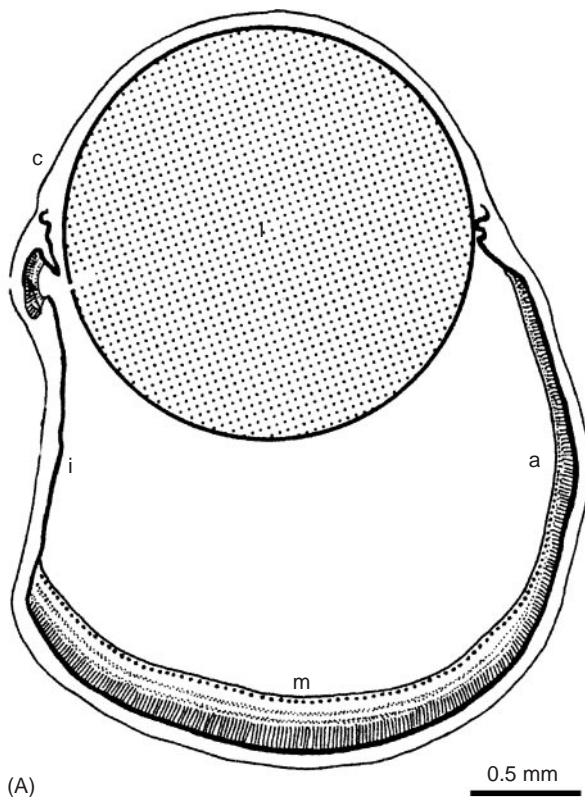


Figure 3 Outline tracing of the lens and retina-choroid border in a stingray (*Dasyatis sayi*), showing the asymmetrical nature of the eye. (From Sivak JG (1980 Accommodation in vertebrates: a contemporary survey. *Current Topics in Eye Research* 3: 281–330.))



(A)



(B)

Figure 4 (A) Camera lucida drawings of resin sections of the tubular eye of *Opisthoproctus grimaldii*: c = cornea; l = lens; m = main retina; a = accessory retina; i = reflective iris. (From Collin SP, Hoskins RV and Partridge JC (1997) Tubular eyes of deep-sea fishes: a comparative study of retinal topography. *Brain Behaviour and Evolution* 50: 335–357.) (B) Lateral view of *Opisthoproctus* sp. showing its tubular eye. (Photograph by N. J. Marshall.)

of diurnal terrestrial animals are generally flattened and less powerful (nocturnal animals tend to have rounder lenses, as well as wider pupils, as their shorter focal length results in a brighter image), the lenses of most teleost fish are spherical. However, some larger-eyed teleosts, as well as many elasmobranchs, do possess somewhat flattened lenses, and

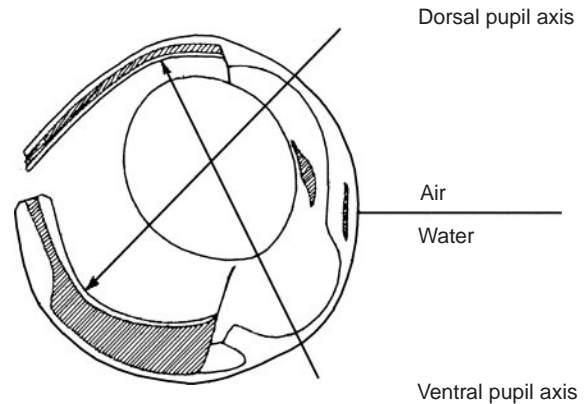


Figure 5 The eye of *Anableps anableps*, half of whose eye lies above water surface and half beneath when the fish is at rest. It is able to see simultaneously in both media by the possession of an aspheric lens positioned such that light entering the eye from the air, and hence going through the refractive cornea, passes through the short axis of the lens and therefore is refracted less. Light from below the animal, passing through the optically ineffective cornea goes through the more powerful long axis of the lens. (From Sivak JG (1976) Optics of the eye of the "four-eyed" fish (*Anableps anableps*). *Vision Research* 16: 531–534.)

the surface-dwelling 'four-eyed' fish, *Anableps anableps*, has an asymmetrical lens to allow simultaneous vision in air and water (Figure 5).

Since the cornea is optically ineffective underwater, the pupil of a fish eye is usually immobile (see below), and the iris does not cover significant parts of the lens, the quality of the lens dictates the optical quality of the whole eye. Two major optical aberrations could theoretically affect the quality of the image produced. First, light entering the lens at different points might be focused at different distances behind it. Such 'spherical aberration' is minimized in fish by a refractive index gradient within the lens (high refractive index in the centre, decreasing toward the edge). Second, since the refractive index of a substance depends on the wavelength of light, different wavelengths will be focused at different points ('chromatic aberration'). Although fish lenses do suffer small amounts of both spherical and chromatic aberration, in general they are of high optical quality. In most species the image quality, and hence visual performance, will be unaffected by these small imperfections, since the lens provides a better image than can be resolved by the retina given its photoreceptor spacing. At rest an eye can be focused in one of 3 ways. Parallel light rays entering the eye either focus on the retina (emmetropia), behind it (hyperopia) or in front of it (myopia). Although determining the refractive state of animals is fraught with difficulty, most are likely to be emmetropic, resulting in a resting eye focused

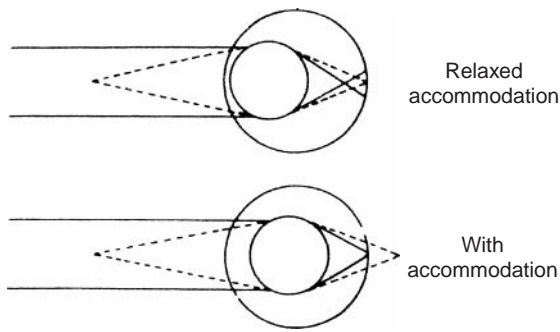


Figure 6 Schematic representation of a 'relaxed' (myopic) teleost eye in which close objects are imaged on the retina, and an accommodated eye in which the lens has moved toward the retina, focusing more distant objects. (From (1980 Accommodation in vertebrates: a contemporary survey. *Current Topics in Eye Research* 3: 281–330.)

from an intermediate distance to infinity. Some teleosts, however, are myopic, with an eye focused for close objects, which, given the often limited visibility underwater, appears appropriate. The suggestion that some elasmobranchs may be hyperopic, resulting in an unfocused image at rest, on the other hand, seems unlikely.

Whatever the refractive state of the resting eye, most animals have the ability to change the point at

which it is focused. While mammals, birds, and reptiles perform such accommodation largely by deforming the shape of their soft lens, and in some instances the cornea, amphibia and fish accommodate by repositioning their hard spherical lenses. In teleosts, one or two retractor lentis muscles (**Figure 1**) contract to pull the lens backward, focusing the previously myopic eye for distance, in some instances by as much as 40 diopters (**Figure 6**), while in at least some elasmobranchs retractor lentis muscles move the lens forward, closer to the cornea.

Pupil

While constriction of the pupil in response to increased illumination is widespread among other vertebrates, in fish it is largely restricted to elasmobranchs. The very few teleosts that have mobile irises are mainly cryptic bottom-dwelling species among whom pupillary closure may serve to camouflage the otherwise very visible pupil. In all such species the dilated pupil is more or less round. However, in many species, when constricted the pupil consists of either a vertical or horizontal slit, a crescent-moon-shaped opening, or even two small pinholes (**Figure 7**). Such irregular pupils may serve a number of functions, for example, the

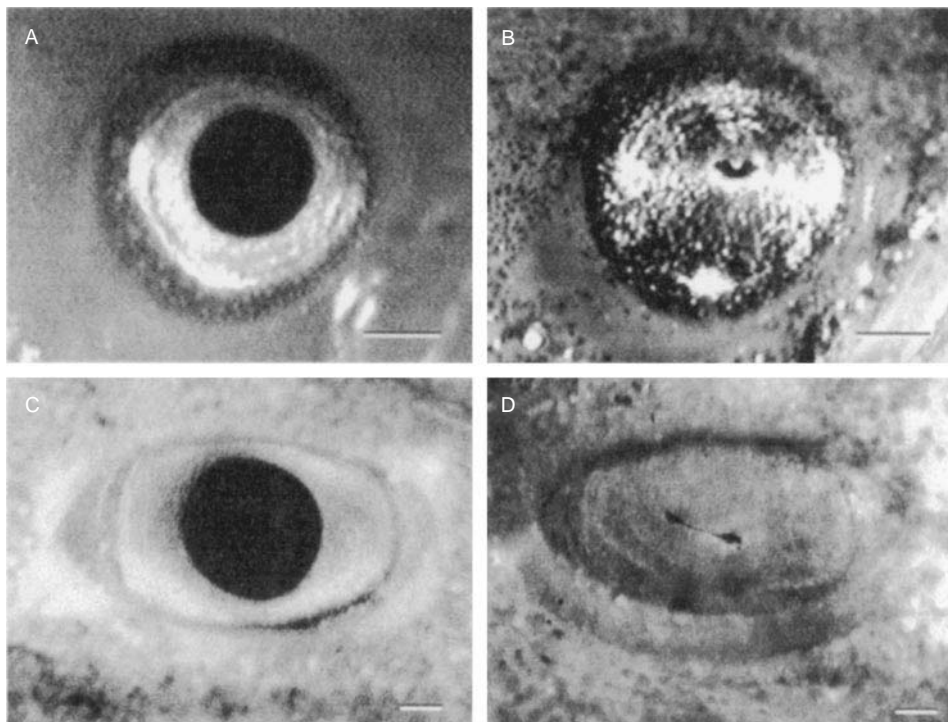


Figure 7 Fully dilated and constricted pupils of the plainfin midshipman *Porichthys notatus* (A and B) and swell shark *Cephaloscyllium ventriosum* (C and D). The scale bar represents 1 mm. (From Douglas RH, Harper RD and Lasa JF (1998) The pupil response of a teleost fish, *Porichthys notatus*: description and comparison to other species. *Vision Research* 38(18): 2697–2710.

maintenance of a small depth of field to facilitate distance judgment using accommodative cues, reduction of chromatic aberration, and spatial filtering of the image.

Ocular Filters

Both water molecules and small particles, such as plankton, suspended in the water column, tend to scatter light, resulting in a greatly reduced range at which fish will be able to see objects. Such (Rayleigh) scatter is particularly severe at short wavelengths. This part of the spectrum is also most prone to chromatic aberration (see above) further degrading the retinal image, and comprises those wavelengths most likely to damage the eye. It is therefore not surprising that short-wave absorbing filters, which often appear yellow to the human observer, are widespread within the corneas and lenses of fish (Figure 8). A similar function is performed by reflective layers in the corneas of some fish resulting in corneal iridescence.

The drawback of such pigmentation is that the overall level of illumination reaching the retina is reduced significantly. Short-wave filters are therefore generally found in diurnal animals inhabiting high light levels. Furthermore, both corneal pigmentation and iridescence are often restricted to, or are densest in, a dorsal region above the pupil. Such 'eyeshades' will selectively reduce the amount of bright downwelling light, while leaving the less intense light, entering the eye along the optic axis, relatively unaffected. Some species have negated the undesirable loss of sensitivity in low light levels by developing 'occlusable' corneas, in which pigment is aggregated around the edge of the cornea in dim light and only migrates to cover the central cornea on exposure to higher light levels. In general animals inhabiting lower light levels lack short-wave absorbing pigmentation and have ocular media that transmit all wavelengths below the infrared down to around 320 nm (Figure 8).

Surprisingly, however, yellow lenses are found in some species inhabiting the deep sea (Figure 8A–D). This is because there are two sources of illumination here; dim residual sunlight, consisting mainly of a narrow band of radiation between 450–480 nm, and bioluminescence produced by most animals in the deep sea. In the mesopelagic zone (200–1000 m), where both bioluminescence and downwelling sunlight may be present, there is a potential conflict in the perception of these two sources. Although both tend to be most intense around 450–500 nm, bioluminescent emissions often contain more long-wave radiation than the surrounding

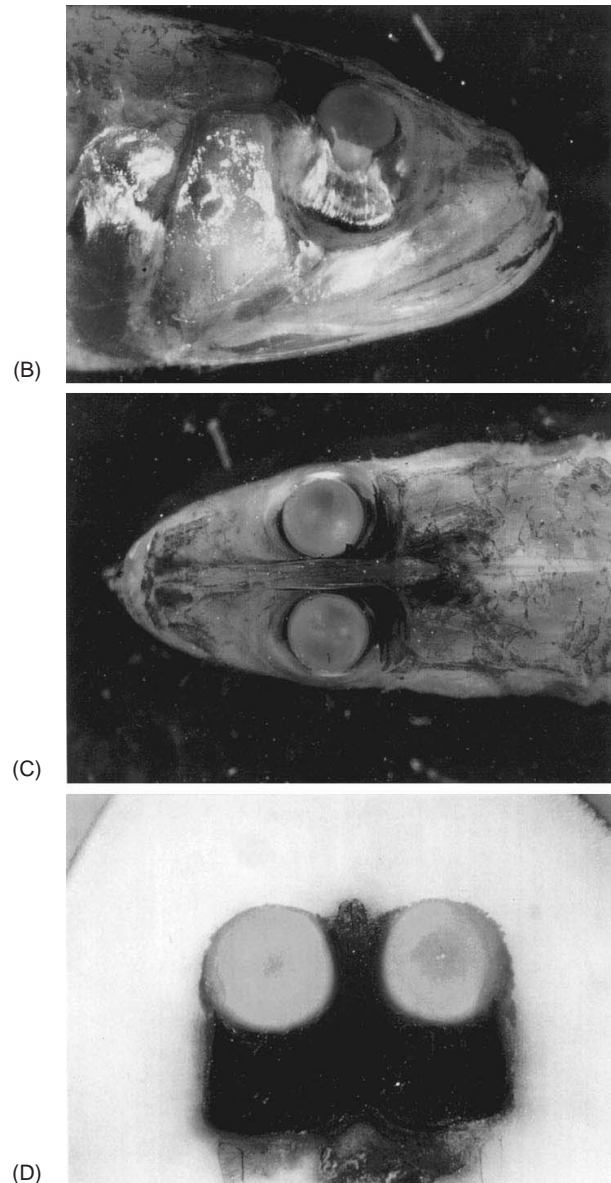
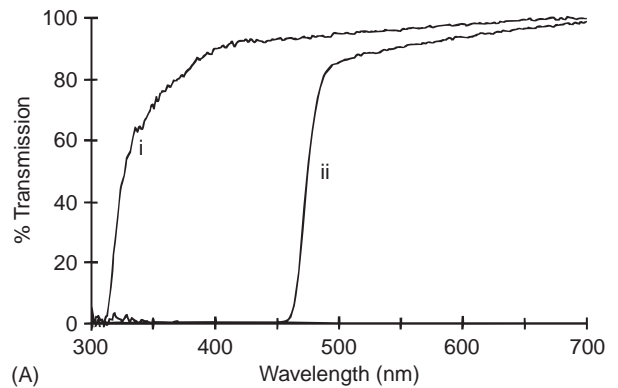


Figure 8 (A) Spectral transmission curves of the lenses of *Opisthoproctus soleatus* (i) whose tubular eye with a 'colorless' lens is shown in Figure 4B and *Scopelarchus analis* (ii) whose tubular eyes with 'yellow' lenses are shown in (B) lateral view, (C) dorsal view, and (D) transverse section. (Photographs by N. J. Marshall.)

spacelight. Short-wave absorbing filters will decrease the intensity of downwelling sunlight more than the relatively long-wave rich bioluminescence, thereby enhancing the contrast of the bioluminescence and making it more visible (see below). At depths below which sunlight has become visually irrelevant (1000m in the clearest waters but much shallower in most water bodies) animals no longer possess pigmented lenses.

Retinal Structure

As in other vertebrates, the fish retina is a layered structure composed primarily of six different nerve cell types (Figure 9). Within this basic framework, however, different species have undergone extensive 'adaptive radiation.'

Species Variation

The majority of vertebrate retinas, including those of most fish, contain two classes of photoreceptor: rods and cones. Cones are employed at higher (photopic) light levels, such as are experienced dur-

ing the day near the water surface, and in most instances mediate high-acuity color vision. Rods are utilized at lower (scotopic) light levels to maximize sensitivity, usually at the expense of chromatic and spatial detail. Not surprisingly, animals habitually exposed to low light levels have increased their sensitivity by developing more extensive rod systems than those living in brighter sunlit waters. For example, freshwater catfish have reduced cones and much enlarged rod outer segments compared to other species (Figure 10). Such specialization is taken to the extreme in deep-sea fish, whose retinas are usually cone-free and in which the rod outer segments have become either extremely long (Figure 11A) or banked into several layers (Figure 11B).

Sensitivity is further increased in some nocturnal or deep-dwelling species by a reflective tapetum behind the photoreceptors, giving rise to the phenomenon of eyeshine (Figure 12). Such tapeta can be located in either the retinal pigment epithelium or the choroid, and may contain a number of different reflecting materials, most commonly guanine. Tapeta are often restricted to the dorsal half of the eye, which receives the lowest-intensity radiation.

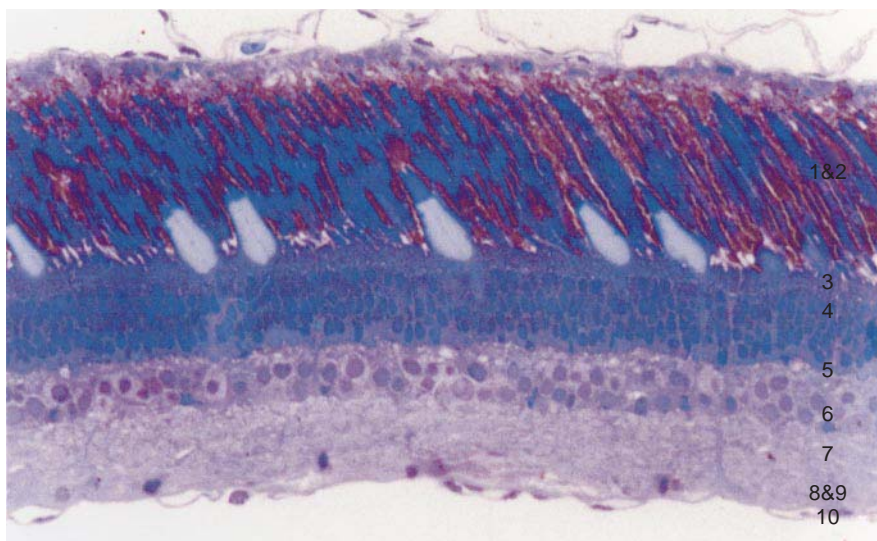


Figure 9 Transverse section of the retina of *Porichthys notatus*. This species displays the 'standard' design of the vertebrate retina divided into 10 layers. (1) Retinal pigment epithelium (RPE). (2) Layer of rod and cone inner and outer segments. As this retina is light-adapted, the melanin within the RPE is dispersed and there is no clear division between layers (1) and (2). (3) External limiting membrane formed by tight junctions between Müller cells and photoreceptors. (4) Outer nuclear layer composed of rod and cone nuclei. (5) Outer plexiform layer composed of synapses between photoreceptors, bipolar, horizontal, and interplexiform cells. (6) Inner nuclear layer comprising cell bodies of horizontal, bipolar, amacrine, interplexiform, and Müller cells. (7) Inner plexiform layer consisting of synapses between bipolar, amacrine, interplexiform, and ganglion cells. This is also the layer in which retinal efferents synapse. (8) Ganglion cell layer composed primarily of ganglion cell bodies but probably also containing some interplexiform and 'displaced' amacrine cell nuclei. (9) Nerve fiber layer containing ganglion cell axons running toward the optic disk. (10) Internal limiting membrane. The fact that *Porichthys notatus* is adapted to life at low light levels is shown by the preponderance of rods and double cones and thin ganglion cell and nerve fiber layers (indicative of convergence and therefore increased sensitivity). The nerve fiber layer is in fact so thin that it is not distinguishable at this magnification. Species inhabiting well-lit environments would tend to have more morphological (and hence spectral) cone types, including single cones, and a thicker nerve fiber layer.

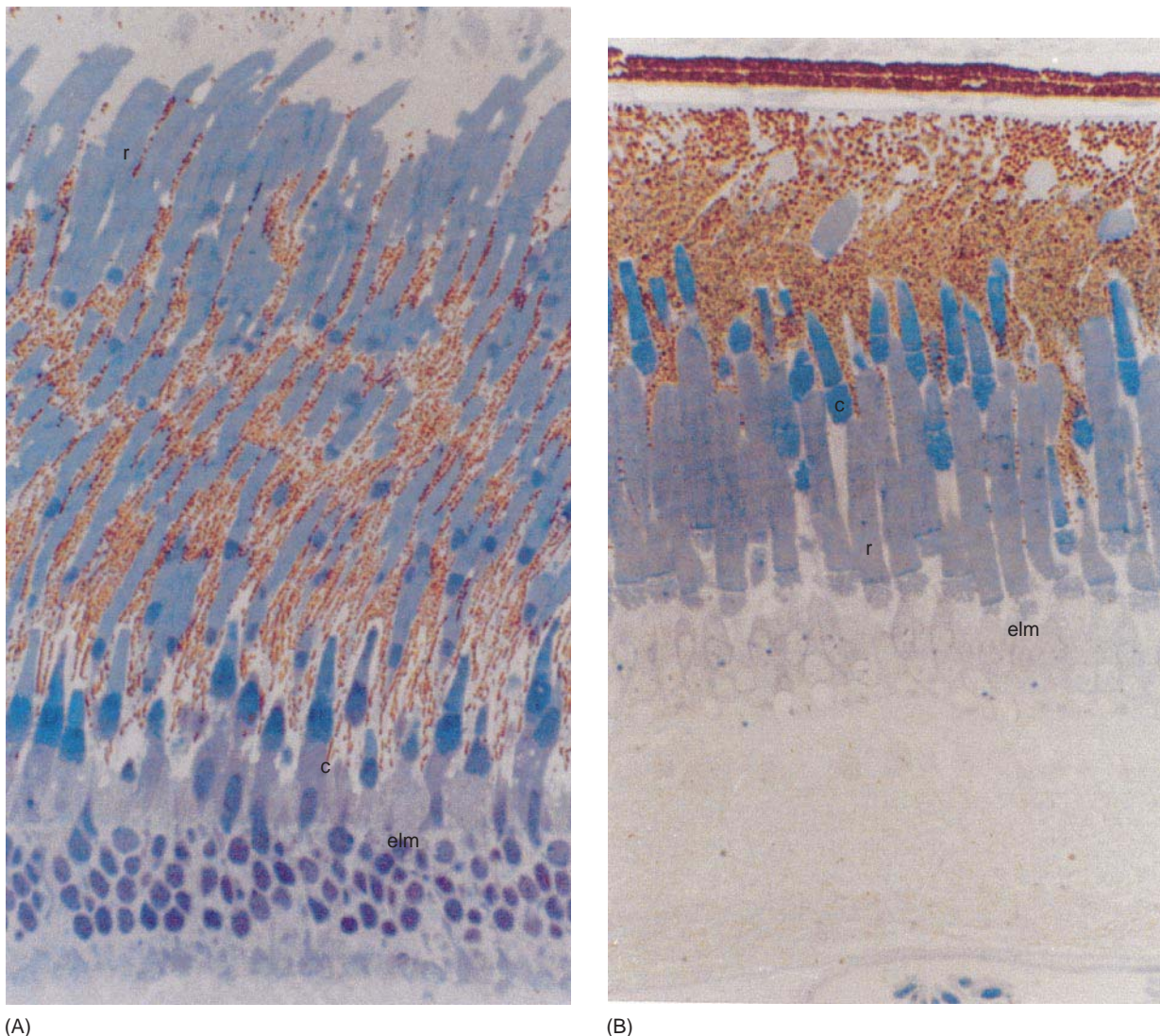


Figure 10 Transverse sections through the retina of (A) the tench (*Tinca tinca*) and (B) a glass catfish (*Kryptopterus bichirris*). Note the relatively larger rod outer segments in the catfish. c = cone; r = rod; elm = external limiting membrane. The rods and cones appear in different positions in the two figures as the tench is light-adapted and the catfish is dark-adapted (see below **Figure 15**).

Since tapeta are usually only beneficial in low light levels and cause image degradation in brighter light, some elasmobranchs have occlusable tapeta in which melanin migrates to cover the reflective material in brighter light.

Most fish, like other vertebrates, contain more than one spectral class of 'single' cone in their retinas (see below). Many fish, like some birds, also have 'double' (**Figures 9** and **13**) and sometimes even triple or quadruple cones. While cones are generally thought to subserve color vision, it is likely that double cones enhance sensitivity. Evidence of a role for the involvement of double cones in increasing sensitivity is provided, for instance, by the

observation that some surface-dwelling fish have retinas containing primarily single cones, but that these are replaced by double cones when the animals migrate to deeper water later in their life cycle. Double cones may also be important in the ability of a fish to see the plane of polarized light (see below).

While the photoreceptors of most animals appear to form no consistent pattern, the cones of many fish are arranged in regular mosaics (**Figure 13**). Although the function of such arrangements is not completely clear, they tend to be observed in species where vision is the dominant sense and have a role to play in polarization sensitivity (see below).

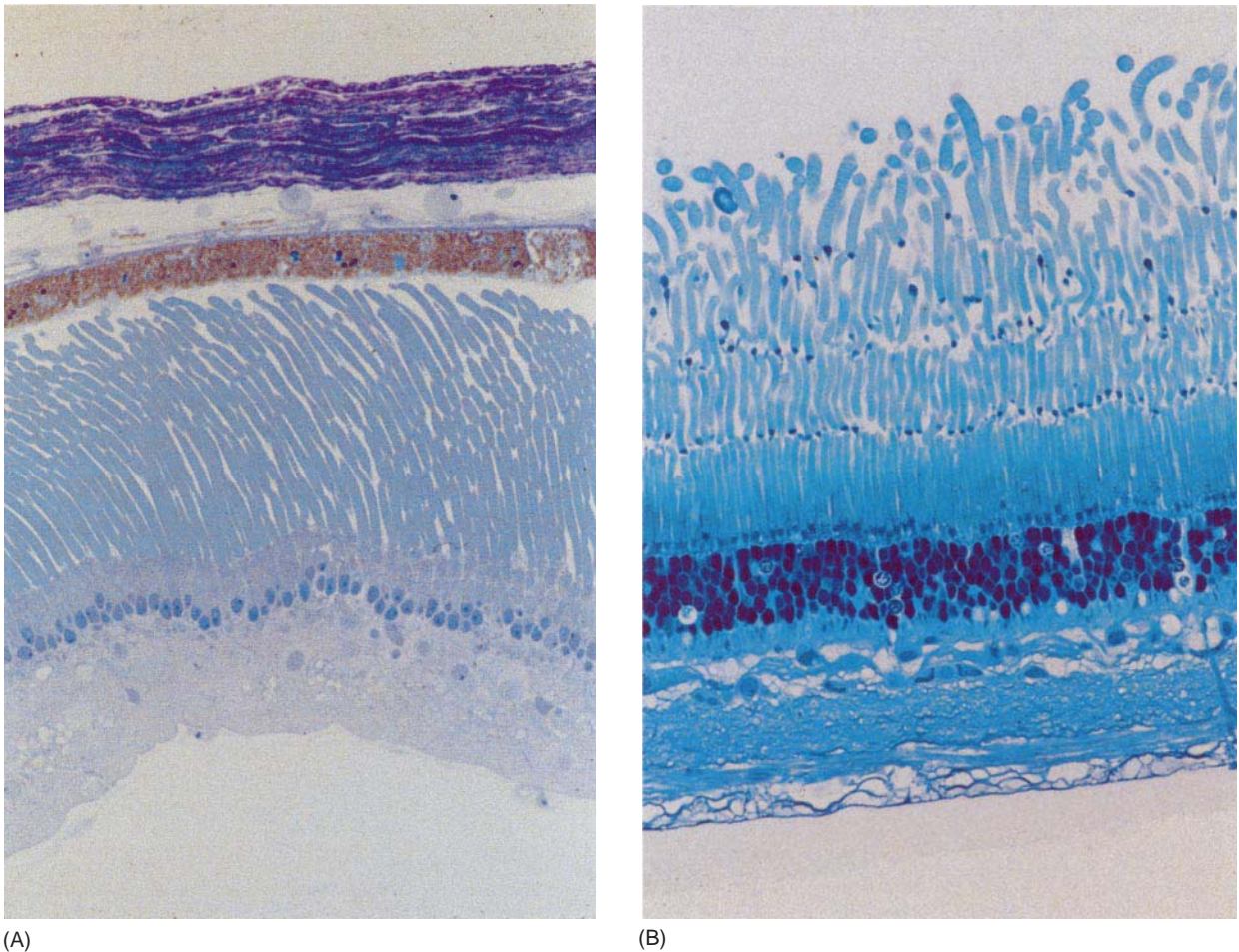


Figure 11 Transverse sections through the retinas of two species of deep-sea fish: (A) *Xenodermichthys copei* displaying a single bank of long rods; and (B) *Notacanthus chemnitzii* with four banks of shorter rods. The RPE has been removed in this section. (Photograph by H.-J. Wagner.)

Many fish show extensive regional variations in retinal structure. Some have a well-developed fovea, comparable to that of humans, where a high density of cones is located in a retinal depression. In other species, a distinct retinal depression may be lacking,

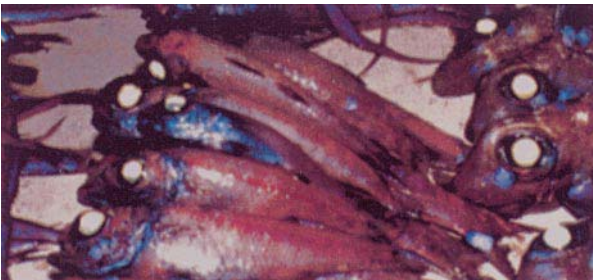


Figure 12 Freshly caught specimens of the benthopelagic *Chimaera monstrosa* photographed with an electronic flash that is reflected by the tapetum lucidum, giving rise to the appearance of 'eyeshine.'

but one still finds 'areas' of high photoreceptor or ganglion cell density. Such regional specializations, which in surface-dwelling species are areas subserving high spatial acuity, can have a variety of different shapes (Figure 14) and be located in quite different parts of the retina depending on the most relevant line of sight and habitat structure for a particular species.

Light and Dark Adaptation

During the course of a normal 24-hour period many fish can be exposed to a wide range of light levels, and those living near the surface experience fluctuations in brightness of up to 10 log units during the course of a day. Despite the fact that the dynamic range of photoreceptors is only about 3 log units at any one time, most species are able to maintain some form of vision throughout all of the light-dark

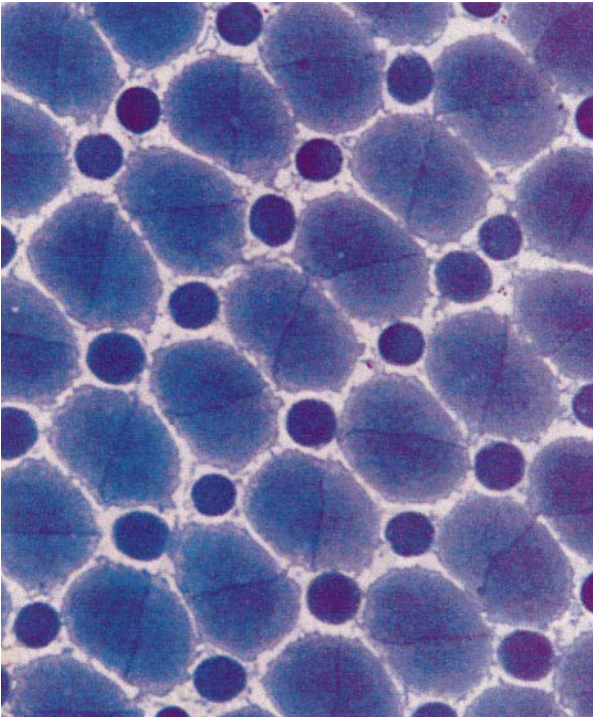


Figure 13 Tangential section through the retina of a rainbow trout (*Oncorhynchus mykiss*) at the level of the cone inner segments. The two members of the double cones (large lighter circles) contain visual pigments with λ_{max} values 531 and 576 nm, while the two types of single cone (small dark circles) contain pigments with λ_{max} 365 and 434 nm. The spatial resolving power (acuity) of the animal is to a large extent determined by the spacing of cones within this 'mosaic'. (From Hawryshyn CW (1992) Polarisation vision in fish. *American Scientist*, March–April: 164–175.)

cycle. This is achieved through adaptive processes that involve a variety of biochemical, physiological, and morphological changes within the retina. In fish the most prominent structural changes that accompany the diurnal light–dark cycle are retinomotor (photomechanical) movements of the rods, cones, and melanosomes within the cells of the retinal pigment epithelium (RPE) (Figure 15). On light exposure, cone myoids contract to position the cone outer segments near the external limiting membrane (ELM) while the rod myoids elongate burying the rod outer segments behind a dense screen of melanosomes that are dispersed within the apical processes of the RPE (Figures 15A, 9, and 10A). In lower light levels these positions are reversed and the rods now lie closest to the ELM, while the cone outer segments are positioned near the choroid along with the melanosomes aggregated at the base of the RPE cells (Figures 15B and 10B). These movements serve primarily to make optimal use of

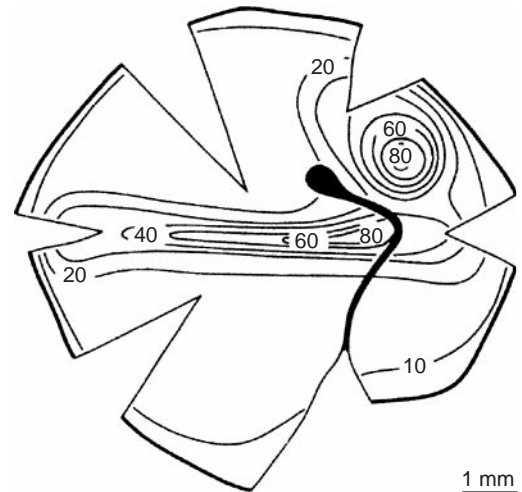


Figure 14 Regional specialization of the blue tuskfish (*Choerodon albigena*) retina. Lines represent isodensity contours ($10^3 \text{ cells mm}^{-2}$) of retinal ganglion cells. The optic nerve head and falciform process are shown in black. This species has both a horizontal 'visual streak,' which could be used to enhance the perception of the 'horizon,' and a temporal 'area centralis,' possibly utilized for imaging prey approaching from the front. (From Collin (1997).)

the retinal space and to protect the rods from being bleached in high light levels.

Visual Pigments

Structure

All visual pigments, which are located within the membranes of the photoreceptor outer segment disks, consist of two components: the chromophore, an aldehyde of vitamin A, which absorbs the light;

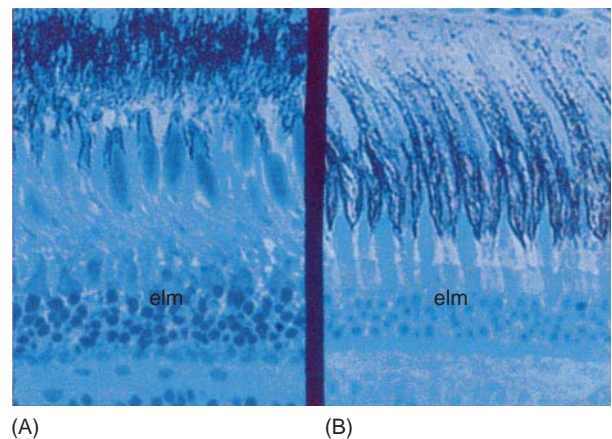


Figure 15 (A) Light-adapted and (B) dark-adapted outer retina of the perch (*Perca fluviatilis*). elm = external limiting membrane.

and a protein, opsin, which determines the spectral absorption characteristics of the chromophore. The chromophore in most vertebrates is retinal, a derivative of vitamin A₁. However, some fish possess an additional chromophore, 3,4-dehydroretinal, derived from vitamin A₂. Visual pigments with retinal as their chromophore are known as rhodopsins, while vitamin A₂-based pigments are referred to as porphyropsins. The retinal photoreceptors of some animals contain 'pigment pairs' in which the same opsin is bound either to retinal or to 3,4-dehydroretinal. A visual pigment consisting of a given opsin and using retinal as the chromophore will have a narrower absorption spectrum peaking at shorter wavelengths than a pigment composed of the same opsin bound to 3,4-dehydroretinal (Figure 16).

All opsins have a similar structure, consisting of a chain of around 350 amino acids that crosses the outer segment disk membrane seven times in the form of α -helices. Isolated retinal and 3,4-dehydroretinal absorb at ~ 380 and 400 nm, respectively. When bound to the opsin, the amino acids 'tune' the chromophore to absorb at longer wavelengths. Thus, the absorption spectrum of a visual pigment depends both on the identity of the chromophore and on the amino acid composition of the opsin surrounding that chromophore.

Spectral absorption

Visual pigments have bell-shaped absorption spectra (Figure 16) that are most easily characterized by their wavelength of maximum absorption (λ_{\max}). Of all classes of vertebrate, fish exhibit the greatest range of visual pigments, with λ_{\max} values from around 350 nm in the ultraviolet to 635 nm in the red, adapting them to the optical diversity of the

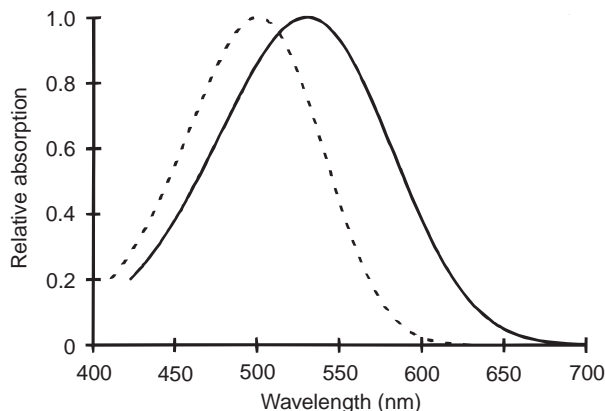


Figure 16 Absorption spectrum of a rhodopsin visual pigment with λ_{\max} 500 nm (dotted) and a porphyropsin (solid) based on the same opsin (λ_{\max} 530 nm) forming a pigment 'pair.'

aquatic habitat, which can vary enormously in its spectral composition depending on the quantity and identity of material dissolved or suspended within it (see Figure 2).

Fresh water, for example, transmits primarily long-wave radiation. Consequently, fish living within it tend to have red-shifted visual pigments compared to those inhabiting oceanic environments where shorter wavelengths penetrate the water most easily. This difference in spectral sensitivity is partly caused by animals in the two environments possessing different opsins, but is also often due to differences in the chromophore. In fresh water many animals use 3,4-dehydroretinal, which, as noted above, forms porphyropsin pigments absorbing at longer wavelengths than rhodopsins, which are the pigments generally used by oceanic animals. Some species, in both the marine and fresh water environment, contain both rhodopsins and porphyropsins in their photoreceptors, and the relative proportions of these two pigment types, for reasons that are both metabolically and ecologically unclear, are influenced by factors such as season, day length, temperature, reproductive state, age, and diet. Interestingly, animals that migrate between fresh water and oceanic environments, such as eels and some salmonids, 'retune' their visual pigments by changing their chromophore accordingly. Eels additionally begin to manufacture a different rod opsin when migrating from rivers to the sea. This opsin produces a short-wave-sensitive visual pigment typical, in spectral absorption, of a pigment in the eyes of deep-sea fish.

The relationship between visual pigment absorption and optical environment can most easily be seen by considering rod visual pigments, whose λ_{\max} values show a gradual shift from the long to shorter wavelength end of the spectrum in animals inhabiting fresh water, coastal, and deep marine environments (Figure 17). While surface-dwelling oceanic species have rod visual pigments with λ_{\max} values close to 500 nm, the vast majority of deep-sea fish have their λ_{\max} within the range 470–490 nm. This hypsochromatic shift is partly an adaptation to the detection of the residual downwelling sunlight, but in most species most probably serves primarily to enhance the perception of bioluminescence. Both residual sunlight and bioluminescence in the deep sea are most intense around 450–500 nm.

The most notable example of visual pigment adaptation to detect bioluminescent emissions is provided by three species of stomiiform dragonfish, which have suborbital photophores producing far-red bioluminescence with peak emissions above

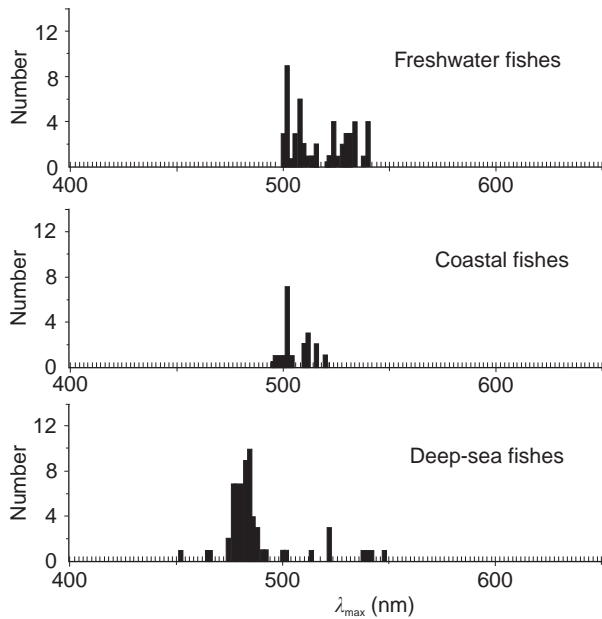


Figure 17 Histogram of λ_{\max} values of rod visual pigments from fish inhabiting three different habitats. (From Partridge JC (1990) The colour sensitivity and vision of fish. In (Herring PJ, Campbell AK, Whitfield M and Maddock L eds) *Light and Life in the Sea*. Cambridge University Press.)

700 nm, that will be invisible to most animals in the deep sea. Two of these genera, *Aristostomias* and *Pachystomias*, are able to perceive their own far-red bioluminescence through the possession of at least three long-wave-shifted visual pigments (Figure 18), while the third, *Malacosteus*, has less red-shifted visual pigments, but long-wave sensitivity is enhanced through the use of a unique chlorophyll-derived, long-wave-absorbing photosensitizer (Figure 19). These dragonfish therefore have a 'private' wavelength enabling them to communicate with one another and illuminate their prey without detection by either predators or prey.

The above discussion has centered around rod photoreceptors. However, with the exception of most deep-sea species, the majority of fish have retinas also containing cones. A few species, such as freshwater catfish (Figure 10B) and some elasmobranchs, have just a single spectral class of cone (Figure 20A). Other fish, such as adult pollack, are dichromats and possess two spectral classes of cone similarly to most mammals (Figure 20B). Many fish, however, like humans, have three cone visual pigments (Figure 20C). The possession of a fourth visual pigment, absorbing in the ultraviolet is also not uncommon (Figure 20D). In general, like rod pigments, freshwater animals have more long-wave-sensitive cone pigments than those inhabiting oceanic environments. Marine fish thus lack the

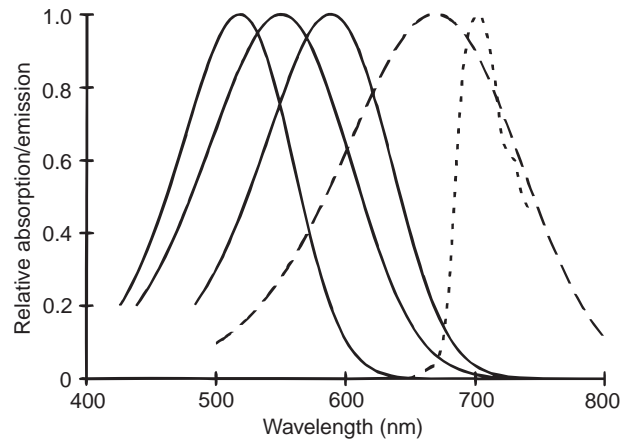


Figure 18 Bioluminescence of the *Aristostomias tittmanni* suborbital photophore (dotted line), and absorption spectra of the three visual pigments (solid lines) so far identified in its retina (a rhodopsin/porphyropsin pigment pair with λ_{\max} values 520 nm and 551 nm and a rhodopsin with $\lambda_{\max} = 588$ nm). The dashed curve represents a fourth visual pigment ($\lambda_{\max} = 669$ nm) believed for theoretical reasons to exist within the retina of this species. (After Douglas *et al.* (1998).)

long-wave-sensitive cones frequently seen in freshwater animals. However, extreme shortwave (ultraviolet) sensitivity occurs among both freshwater and marine teleosts.

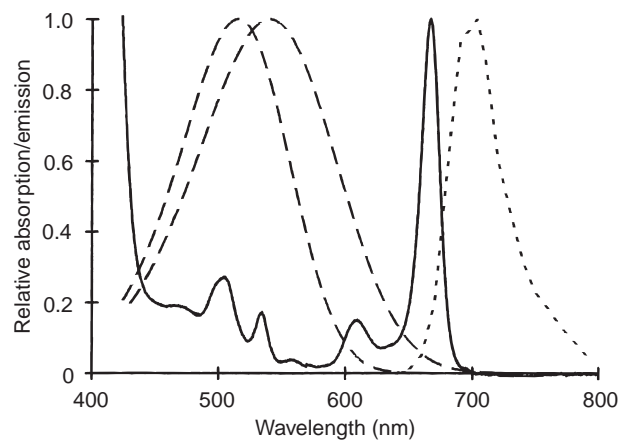


Figure 19 Absorption spectra of the two visual pigments of *Malacosteus niger* (a rhodopsin with $\lambda_{\max} = 515$ nm and a porphyropsin with $\lambda_{\max} = 540$ nm; dashed curves) and of a chlorophyll-derived photosensitizing pigment located within the outer segments of this species (solid line), as well as the bioluminescent emission spectrum of a long-wave-emitting suborbital photophore (dotted line). The bioluminescence, which is unlikely to be absorbed by the visual pigments directly, is initially absorbed by the photosensitizer, which then activates the visual pigments through some as yet undefined mechanism. (Douglas RH, Partridge JC, Dulai KS, Hunt DM, Mullineaux CW and Hynninen PH (1999) Enhanced retinal longwave sensitivity using a chlorophyll-derived photosensitizer in *Malacosteus niger*, a deep-sea dragon fish with far red bioluminescence. *Vision Research* 39: 2817–2832.)

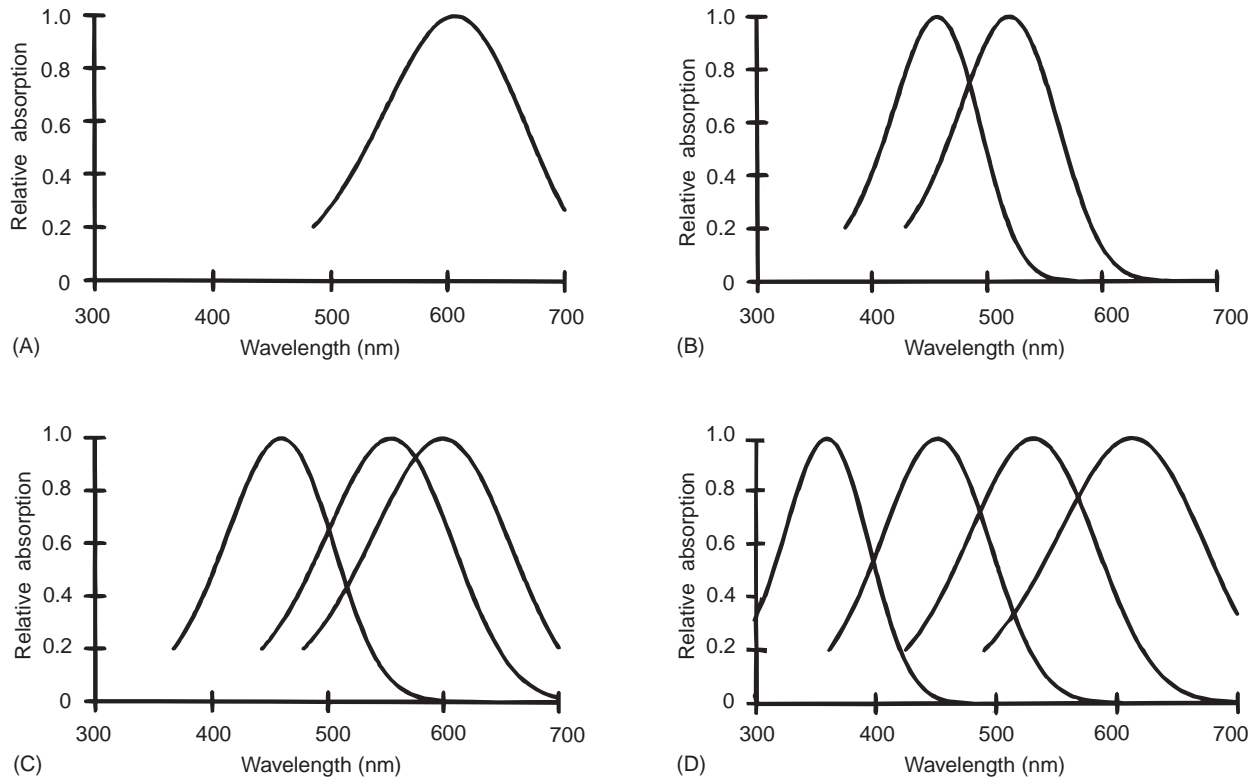


Figure 20 Cone visual pigment absorbance spectra of various teleost fish. (A) Glass catfish (*Kryptopterus bicirrhitis*), which possesses only one spectral class of cone ($\lambda_{\max} = 607$ nm). (B) A ‘dichromatic’ adult pollack (*Pollachius pollachius*) (λ_{\max} 458 nm, and 521 nm). (C) The ‘trichromatic’ cichlid *Nannacara anomala* ($\lambda_{\max} = 460$ nm, 555 nm, and 600 nm). (D) The ‘tetrachromatic’ goldfish (*Carassius auratus*) ($\lambda_{\max} = 360$ nm, 452 nm, 532 nm, and 614 nm). (After Douglas Dauglas RH (2001) The ecology of teleost visual pigments: a good example of sensory adaptation to the environment. In (FG Barth and Schmid A, eds) Ecology.)

All of the above arguments assume that optimum advantage is bestowed upon the animal if the λ_{\max} of the visual pigment matches the predominant wavelength in the surrounding environment. However, such a ‘sensitivity hypothesis’ may not always be appropriate. A visual pigment with a λ_{\max} ‘offset’ from the spacelight would enhance the contrast of relatively bright objects with a different spectral radiance to the background (see below).

Visual Abilities

Vision has a major role to play in many aspects of fish behavior, from locating and attracting a mate to ensuring an adequate food supply and orientating in space. The importance of vision, and the constraints it may place on a behavior, can only be assessed by examining the visual capabilities of the animal.

Detection

The most fundamental task of a visual system is to detect the stimulus. In certain conditions, such as a deep-sea fish viewing a bioluminescent source

against a dark sunless background, this means increasing absolute sensitivity by catching as many photons as possible. However, in most cases an object is viewed against an illuminated background and the task of the visual system is to detect the contrast between stimulus and background.

Absolute sensitivity The absolute sensitivity of a fish depends on the level of background illumination, which in most instances correlates most directly with the time of day. Sensitivity (one/threshold) is high when ambient illumination is low, while in high light levels, when capturing photons is not at a premium, sensitivity is reduced. In animals that possess both rods and cones, this involves switching between one receptor type and another, which, as already outlined above, in fish involves retinomotor relocation of the photoreceptors. Several studies have shown that fish as diverse as goldfish and lemon sharks have a dark-adapted sensitivity exceeding that of humans. In deep-sea fish, with their larger outer segments, reflecting tapeta and higher convergence ratios (pooling the output of rods together), this sensitivity is likely to be en-

hanced even further. Thus, in ideal conditions humans can see sunlight down to a depth of around 850 m in the clearest oceans, while some fish may perceive vestiges of sunlight down to around 1000 m. As the ontogenetic formation of rods lags behind that of cones in fish, many larval retinas possess only cones, and sensitivity therefore increases during development.

Contrast Given a sufficient amount of light to see by, the next most important task for a fish is probably to detect the stimulus at the greatest possible distance. An object only becomes visible when the observer can detect a difference between it and the background. Such contrast detection is especially problematical under water as contrast is severely degraded by both light absorption and scattering; the visual environment underwater has been likened to a 'colored fog'. Some species, when the spectral composition of the background and image-forming light differ, improve contrast by filtering out the background using either intraocular filters or visual pigments with λ_{max} values 'offset' from the background radiance.

A measure of a fish's sensitivity to contrast is the minimum difference between the radiance of an object (R_o) and its background (R_b) that the animal can detect as a function of background radiance (R_b). This measure ($(R_o - R_b)/R_b$), the Weber fraction, ranges between 0.3% and 7.0% in various teleosts at threshold, which is somewhat higher than values ($\sim 1\%$) noted for humans under comparable conditions. The Weber fraction generally decreases at higher levels of background irradiation. Therefore, small percentage changes in brightness are easier to discriminate at higher light levels.

Spatial Resolution

The ability to resolve fine detail may be important to a fish for any number of reasons; for instance to recognize an animal by its body markings, or to react to a prey item at a maximum distance. The simplest way to define the ability of a fish to resolve detail is to determine the angle formed at the eye by two objects that the animal can just recognize as being separate. The value of this minimum resolvable angle varies greatly between species. Thus, the yellowfin tuna (*Thunnus albacares*) has a minimum resolvable angle of 3.7 minutes of arc, while other species can have values as high as 20 minutes of arc. Such variations are closely related to the density of photoreceptors (Figure 13) and ganglion cell spacing. Humans, under comparable conditions, have a minimum separable angle of around 1 minute of

arc. In most species acuity will increase with age, as increased eye size and continued addition of new photoreceptors results in the image being sampled by more cells in older animals, who will therefore, for example, be able to see smaller prey and be able to detect them at greater distances than younger animals.

To achieve high acuity, not only must different parts of the retinal image be sampled by different photoreceptors but the signals generated by these cells have to be kept apart in subsequent neural processing. Consequently, at high light levels, when cones are being used, acuity is high because the cone system displays relatively little neural convergence. However, one of the factors that ensures enhanced sensitivity of the system of rods is their high convergence ratio with postreceptoral neurons. This inevitably leads to a decrease in spatial acuity at low light levels. Although individual photoreceptors are stimulated by different parts of the visual image, this spatial information is lost as the output of all these cells is combined.

Spectral Responses

As noted above, fish have the broadest range of visual pigments of any animal and many behavioral and electrophysiological studies have shown fish to be sensitive from the near ultraviolet (~ 320 nm) to the far red (~ 800 nm). The lower limit is set by the absorption of the ocular media (see above) and the upper limit by the sensitivity of the visual pigment.

To prove that an animal possesses color vision, one has to show that it can discriminate stimuli of different colors irrespective of their brightness. Such behavioral experiments are difficult to perform and the only fish shown to discriminate color in this way has been the goldfish. However, since most fish possess more than one spectral class of cone, and many have been shown to respond to a wide variety of monochromatic stimuli, it is very likely that the vast majority of fish do perceive color.

Distance Perception

While spatial acuity and color sensitivity are perhaps the most important attributes of vision that allow identification of potential predators, prey and conspecifics, in order to respond appropriately to them it is also important to know both their size and distance.

The simplest way to judge the distance of an object is to measure the angle it subtends on the retina, closer objects appearing larger. However, this is only appropriate if the size of the object is known. Thus, some fish, when using a

constant-sized landmark to locate a food source rely solely on visual angle for judging its distance. However, in most situations, if animals estimated distance based purely on visual angle, confusions would continuously arise. A small animal close by, which might provide a potential meal, could be confused with a larger, more distant, predator, because both would subtend the same visual angle. The ability to judge true size, taking distance into account is known as size constancy. Although size constancy has only been demonstrated in goldfish, it is hard to believe that it is not an ability common to most fish.

Polarization

Light has three variable attributes: intensity, frequency (wavelength), and polarization. While the first two of these have been extensively studied (see above), the plane of polarization, like ultraviolet sensitivity, is often forgotten, largely one assumes because humans are unable to detect it. However, there is now considerable evidence that several species of teleost display polarization sensitivity. This appears to rely on the use of double and ultraviolet-sensitive single cones within a regular photoreceptor mosaic (e.g., **Figure 13**), and fish are able to use this information for, among other things, spatial orientation and navigation.

See also

Bioluminescence. Inherent Optical Properties and Irradiance.

Further Reading

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FISHERIES AND CLIMATE

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Every living organism responds in some way to variations in its physical environment. Fish are no exception. Variations in climatic and oceanographic conditions can lead to changes both in the geographical distribution of fish populations and in their dynamics. For obvious reasons, distributional shifts are most dramatic near environmentally controlled limits of species ranges. Perhaps the best-known example is the response to the warming of the north-east Atlantic between the 1920s and 1960s. This warming, which was related to the strengthening of the Greenland high pressure system, was marked by the appearance of subtropical species, like albacore and swordfish, at high latitudes and the return of cod and haddock to the

Barents Sea. Climatic effects on the distribution of a particular species can operate directly by altering the geographic range of physiologically tolerable conditions or indirectly by altering the distribution of prey species.

These examples illustrate occasions when the effects of climatic change can be related to presumptive causes. For most fish stocks, however, explanations of population variability in terms of climate are not so simple. The critical time in the life cycle that determines population size of fish stocks is the period from egg production, through the larval phase to accession of juveniles to the adult population. This ‘recruitment’ process, when numbers of offspring per parent can decrease dramatically – by factors of 10^{-3} to 10^{-5} – is the most variable but least understood part of the life cycle. Yet predicting recruitment is central to the problems of managing commercial fish stocks.

Empirical studies of the relationship between climatic and oceanographic variables and measures of