# BIOLOGY OF FISHES

## FISH 311

## FORM AND FUNCTION, SENSORY MECHANISMS III: EYES AND VISION; VISUAL PIGMENTS; COLOR VISION

**General topics:**

1. Eye structure
2. Image formation and accommodation
3. Light and dark adaptations
4. Visual pigments and color vision

# EYES AND VISION

## 1. EYE STRUCTURE

The eyes of vertebrates are all built on the same basic plan but those of fishes are characterized by a number of **unique structural adaptations** that allow them to function properly in an aquatic medium. The major features of the eye include an **anterior chamber** (filled with a liquid, called **aqueous humor**), an **iris**, a **lens**, and a **posterior chamber** (containing a liquid, called **vitreous humor**), lined by a multi-layered network of **light-sensitive cells**, called the **retina**.

The **spherical lens**, protruding through the **pupil** and forming a boundary between the anterior and posterior chambers, is nearly in contact with the **cornea**, which is essentially a transparent section of the outer layer or **scleroid coat** of the eyeball. The lens is suspended above and held in place by a **suspensory ligament**.

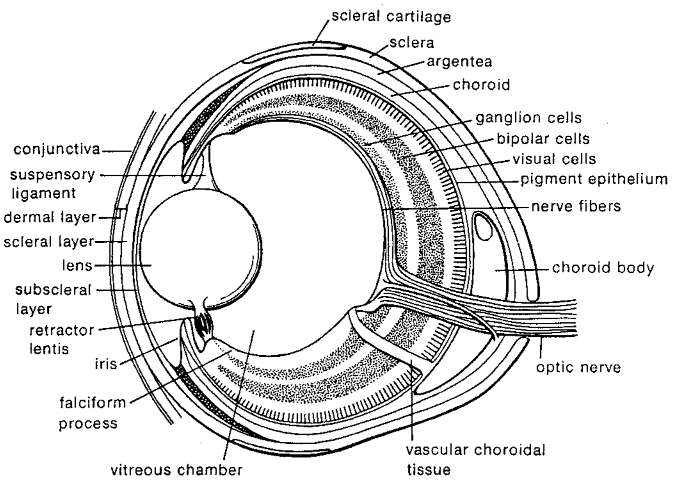


Diagram of vertical section of teleost eye (not drawn to scale), showing the relationships of its parts.

Between the **retina** and the **scleroid coat** (**sclera**) is a highly vascularized **choroid layer**, which functions primarily to nourish the retina but also serves to absorb stray light or in some species to reflect light back through the retina. A **choroid body** or "gland," actually a **rete mirabile**, is prominent in the **choroid layer** of many teleosts (as well as the bowfin); its structure and function is similar to that of the **gas gland** of the teleost swimbladder, serving to provide a high partial pressure of oxygen to the retina.

Fishes have no **eyelids** (and thus cannot close their eyes) except for the **nictitating membranes** of certain sharks. A few elasmobranchs can control the opening of the **pupil** by means of muscles associated with the **iris**, but most fishes lack this control or have it only poorly developed.

The **retina** consists of an outer pigmented epithelium, the **visual cells** (**rods** and **cones**), a layer of bipolar cells and, closest to the posterior chamber, the **ganglion cells** and the **nerve fibers** leading to the **optic nerve**.

## 2. IMAGE FORMATION AND ACCOMMODATION

Fishes live in a medium that has greatly different optical properties than that of air. Depending on the **angle of incidence** of light, a calm water surface can reflect up to 80% of the light striking it. If the water is rough there is great variation in the transmission of light regardless of the angle of incidence. The **refraction** or bending of light rays entering water is such that a fish in water with a perfectly smooth surface views objects above the water through a circle subtended by a 97.2° cone above each eye.

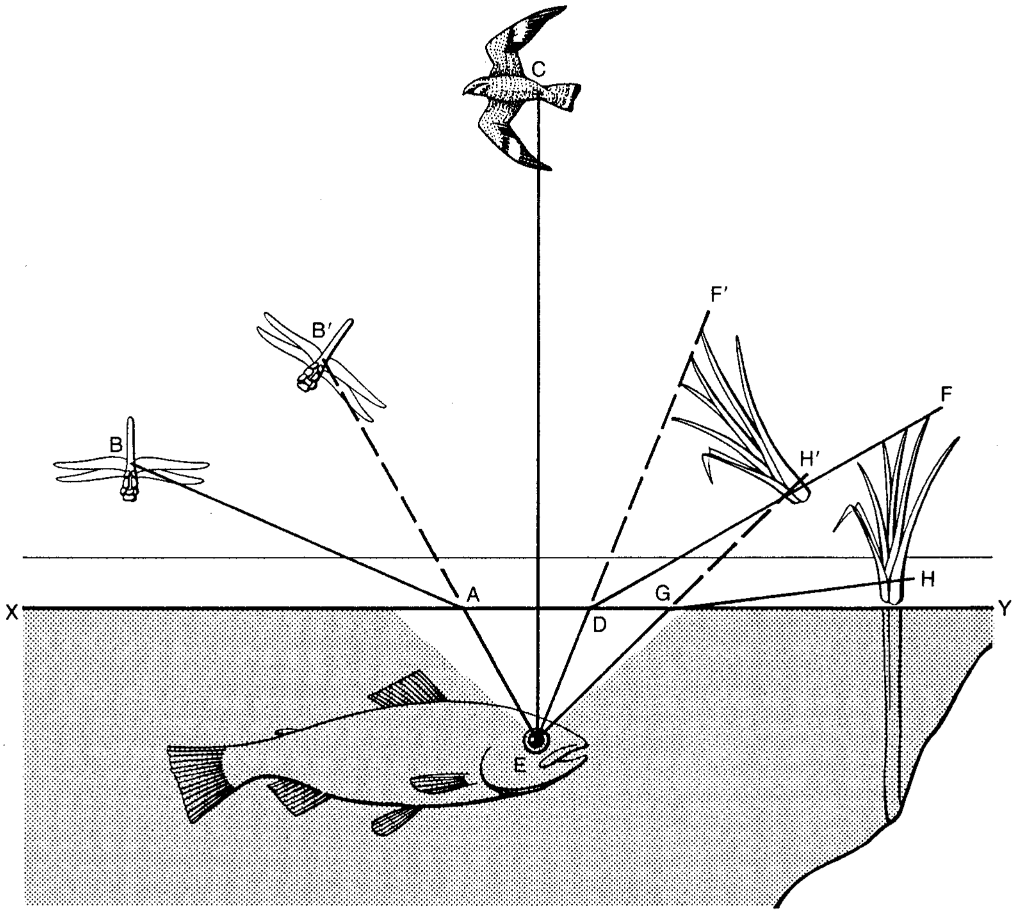


Diagram showing refraction of light entering water with a perfectly flat surface (*XY*). Because of the bending of the light rays, the fish's eye (*E*) does not receive light striking the surface above the shaded area. The bird at *C*, directly above *E*, is seen in its actual position. The insect at *B* is perceived as if at *B'*, and the angles *EDF* and *EGH* cause the plant to be seen as if the top were at *F'* and the bottom at *H'*.

Nearly all objects from horizon to horizon appear in the circle, which is surrounded by the reflective under-surface seen beyond the limits of the cone. In rough water the **circular window** in the surface is broken up and light is transmitted through ever-changing patterns.

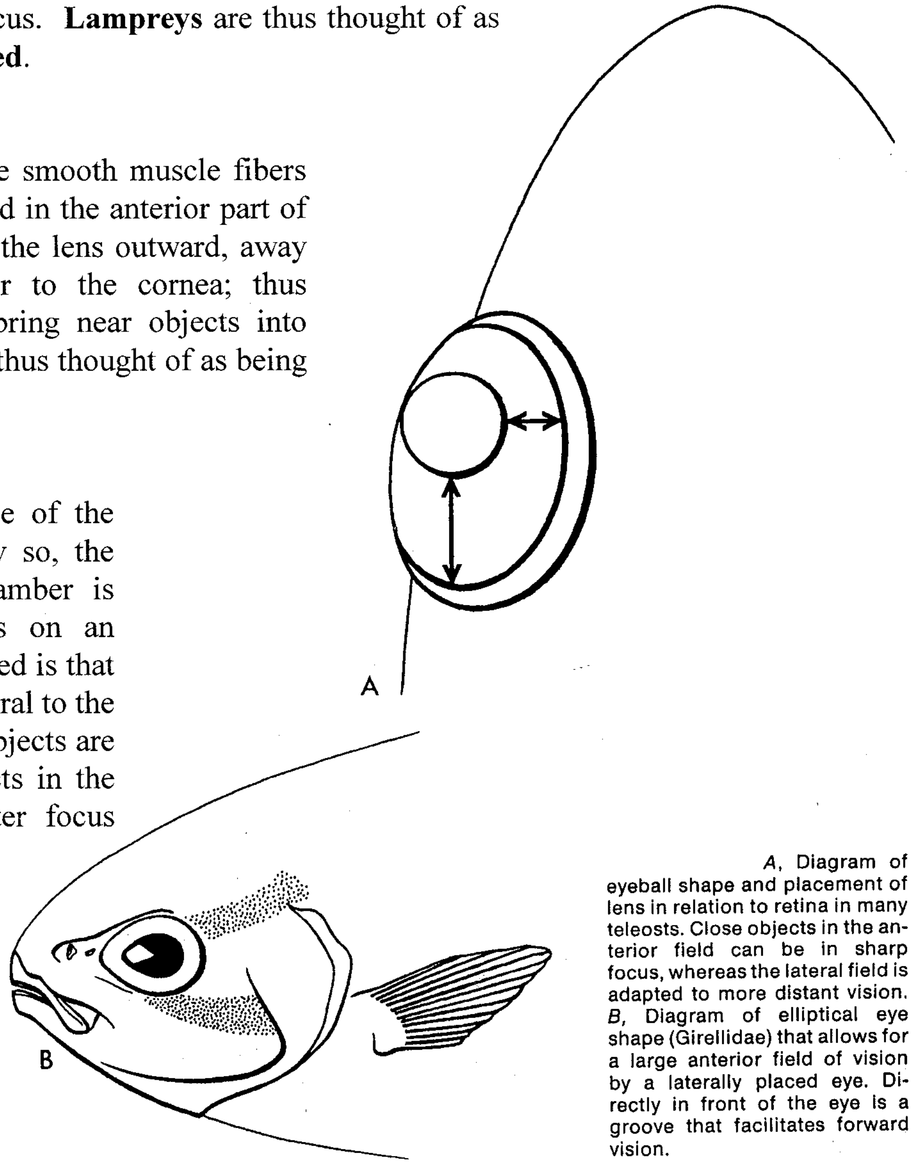
Vision of underwater objects is a different story. In most fishes, the maximum field of view is achieved by placement of the **lens** so that it bulges through the opening of the **pupil** and nearly touches the **cornea**. The lens can thus gather light practically from an entire hemisphere. The **index of refraction** of the cornea is about the same as that of water (1.33), thus it does not bend light. **Refraction** and **image formation**, therefore, depend almost entirely on the lens. The lens is spherical, with a very high **index of refraction** (about 1.67).

In contrast to tetrapod eyes, in which **accommodation** for near and far vision is accomplished by changes in the shape of the lens, the eyes of fishes accommodate by slight anterior and posterior movements of the lens that change the distance between the lens and the retina. The process by which the distance between lens and retina is modified differs among the major groups of fishes:

**Lampreys** have a unique **corneal muscle** that inserts on the outer transparent covering of the eye. When it contracts, the cornea is flattened, pushing the lens inward, closer to the retina and bringing more distant objects into focus. **Lampreys** are thus thought of as being **myopic** or **near-sighted**.

In **elasmobranchs**, there are smooth muscle fibers (**protractor muscles**) located in the anterior part of the **choroid layer** that pull the lens outward, away from the retina and closer to the cornea; thus accommodation serves to bring near objects into focus. **Elasmobranchs** are thus thought of as being **hyperopic** or **far-sighted**.

In **teleosts**, while the shape of the lens is **spherical**, or nearly so, the shape of the posterior chamber is such that the retina takes on an **ellipsoid**. The effect achieved is that relatively distant objects lateral to the fish are in focus but close objects are not. Anteriorly, near objects in the binocular field are in better focus than more distant objects.



*A*, Diagram of eyeball shape and placement of lens in relation to retina in many teleosts. Close objects in the anterior field can be in sharp focus, whereas the lateral field is adapted to more distant vision. *B*, Diagram of elliptical eye shape (Girellidae) that allows for a large anterior field of vision by a laterally placed eye. Directly in front of the eye is a groove that facilitates forward vision.

In **teleosts**, accommodation to distant vision in the anterior field is accomplished by moving the lens backward by means of a **retractor muscle** (**retractor lentis**). Teleosts are thus thought of as being **hyperopic** or **far-sighted** being **myopic** or **near-sighted**.

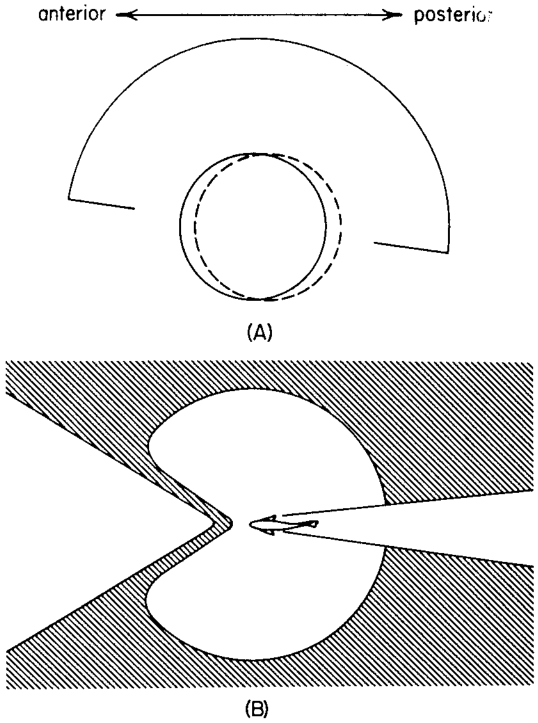


Fig. 2. (A) Diagrammatic horizontal section of the left eye in relation to the longitudinal axis of the fish's body, ↔. Position of the lens at rest (solid line) and in full accommodation (broken line). (B) Diagrammatic representation of the horizontal visual field of a fish, eyes unaccommodated, showing the area in focus (diagonal lines). The triangular open area in front of the fish lies beyond the "far point"; the circular open area to the sides is within the locus of the "near point" (interrupted posteriorly by the shadow of the fish's body).

The ability to accommodate for near and far vision varies considerably among teleosts: in general, most **marine teleosts** have well developed lens muscles and accommodate very well; most **freshwater species** have less well-developed muscles and only moderate powers of accommodation.

## 3. LIGHT AND DARK ADAPTATIONS

Regulation of light as it enters or after it enters the eye, and adaptation to light or dark, are accomplished in a number of ways:

1. One means of regulating light that enter the eye is to **swim to or away** from the source of illumination.

2. Some fishes have **pigment in the cornea or lens that acts as a filter** to eliminate certain wavelengths.

3. Most elasmobranchs and a few teleosts have **contractile irises** that control the amount of light entering the eye.

4. Most rays, many flatfishes, stargazers (family Uranoscopidae), and some catfishes have a **pupillary operculum** that can expand and cut off most of the light reaching the pupil.

5. Some sharks have **nictitating membranes** that can be drawn across the eye to reduce excessive illumination.

6. Light and dark adaptation in teleosts is largely accomplished by **movements of pigment and visual cells** (rods and cones).

# LIGHT AND DARK ADAPTATION IN TELEOSTS

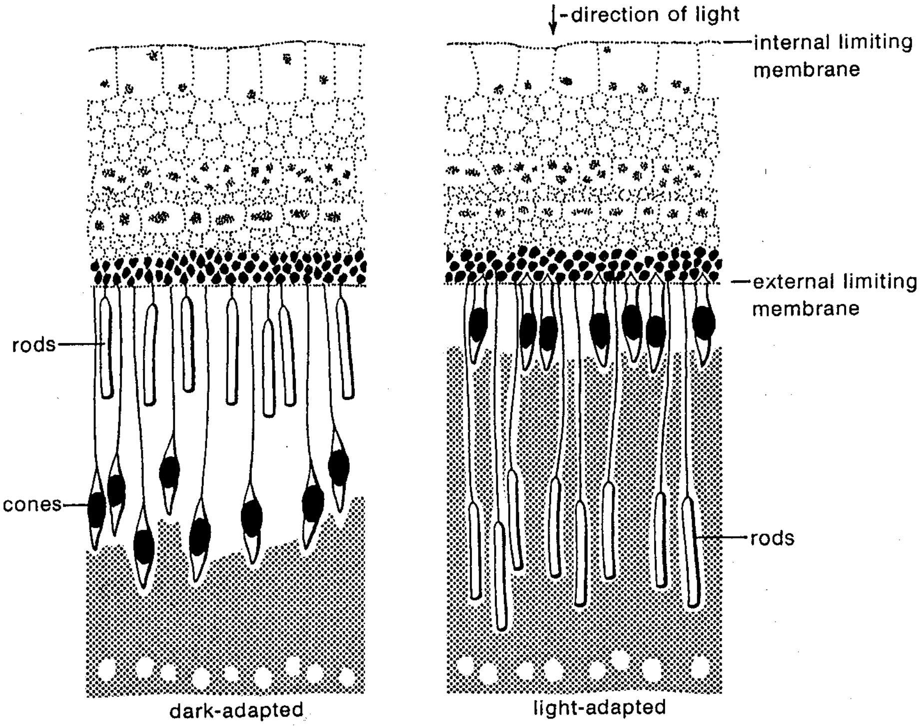


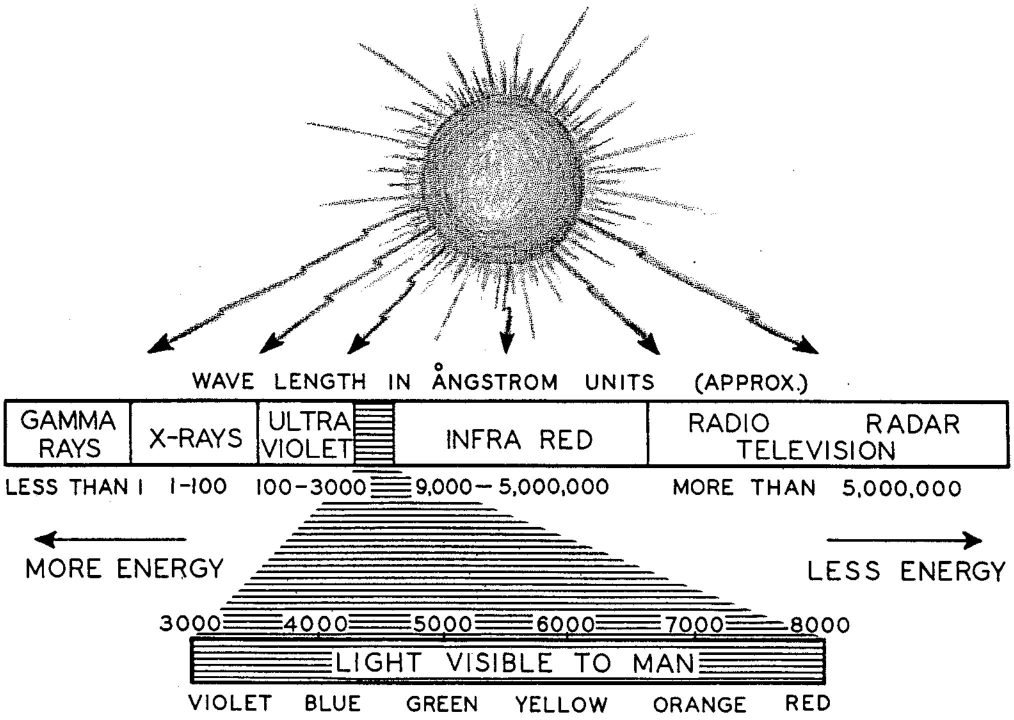
Diagram illustrating movement of rods, cones, and pigment in the retina of teleosts. In light adaptation (*right*) the rods are moved away from the light and are protected by forward movement of pigment.

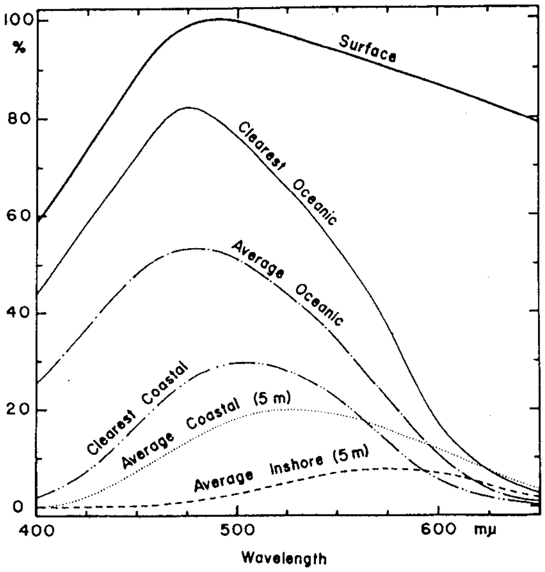
**Pigment cells** in the outer layer of the retina contain processes through which **melanin** can move to or from the outer parts of the visual cells. **Under bright illumination**, the eye adapts by movement of **melanin** toward the visual cells, and by movement of the outer segments of the **rods** into the pigmented area where they are shielded from the light. **In dim light**, the pigment is drawn back and the contractile part of the **rods** pulls them away, exposing them to the light. Movement of the **cones** is opposite that of the rods, but the **cones** are not usually hidden by the pigment. The time required for the shifting of pigment and visual cells in teleosts is considerable: generally, about 30 minutes for light adaptation and an hour or more for dark adaptation.

# 4. VISUAL PIGMENTS AND COLOR VISION

The distribution of **solar radiation** that strikes the earth is relatively **homogeneous**; while the atmosphere does absorb light at the high and low ends of the visual spectrum, its effect is much less significant than that of water.

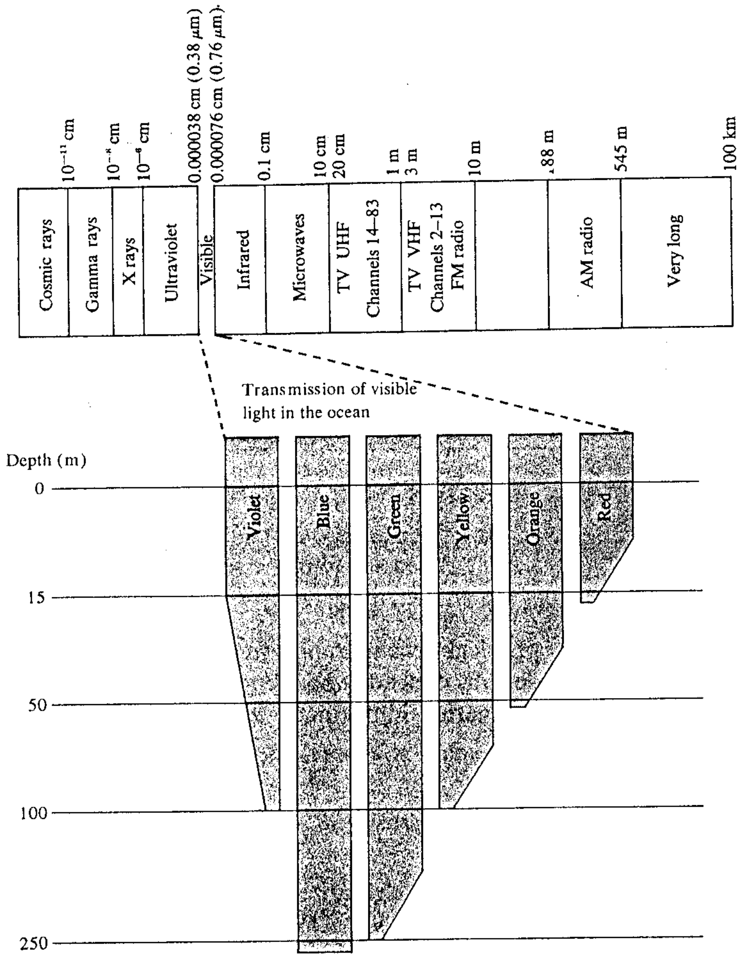
**RADIATION SPECTRUM OF THE SUN**





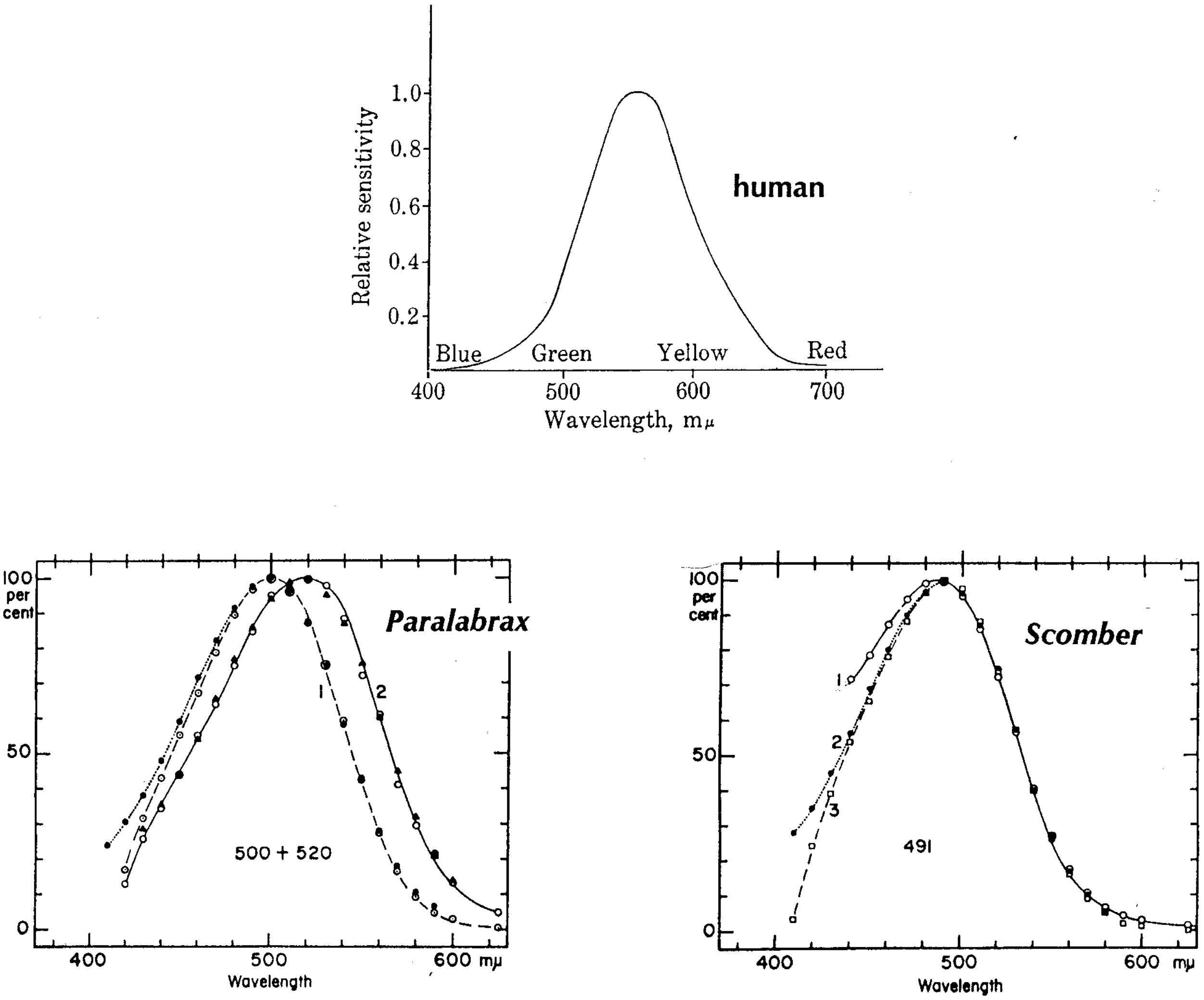
Relative spectral distribution of solar energy in different types of sea water. Ordinate in relative energy units, expressed as percentage of the maximum energy incident at earth's surface.

Water, in contrast to air, absorbs light rapidly and differentially, with colors at the long or red end of the **visual spectrum** attenuating rapidly, and those at the short or blue end, penetrating to relatively great depths. Thus, unlike terrestrial animals, fishes live in a wide range of visual environments, varying particularly in **spectral quality** and **turbidity**.



TRANSMISSION OF VISIBLE LIGHT IN THE OCEAN

Pigments, called **visual pigments** or **retinenes**, associated with the **photoreceptor cells** (i.e., **rods** and **cones**), are responsible for absorbing light; different pigments absorb different wavelengths of light; the distribution of pigments present in the retina of a fish determines its sensitivity to various colors.



Visual sensitivity curves for the **normal human eye** (upper), an intertidal marine fish, ***Paralabrax clathratus*** (lower left), and a marine epipelagic species, ***Scomber japonicus*** (lower right)

Many studies have attempted to relate the **visual pigments** of different species of fishes to the **visual tasks** they face in their particular environments. While these studies have revealed an enormous amount of complexity and variation even, in some cases, within individuals of the same species, some general rules appear to hold:

1. **Deep-sea species** have rod pigments that absorb maximally at relatively short wavelengths (roughly 470 to 490 nm) compared with shallow-water and freshwater species. This is correlated with the predominantly short wavelengths of light that penetrate into their environment. In most cases all the receptors have the same visual pigment, but in a few species two pigments are present, segregated into separate rods. These paired pigment species are usually dark in color as opposed to silvery, and often have specialized bioluminescent organs emitting light of relatively long wavelength, and it has been suggested that the presence of two pigments is related to these factors.

2. **Marine fishes living at intermediate depths** in coastal waters usually have two cone pigments (apart from the rod pigments) that absorb maximally at around 460 and 540 nm, respectively.

3. **Freshwater fishes living near or on the bottom**, particularly if they are crepuscular or nocturnal, also often have two cone pigments, absorbing maximally at around 530 and 620 nm. In both cases the long wavelength cones match the spectral quality of the light fairly well.

4. **Freshwater fishes living in shallow waters** have three cone pigments, two of them similar to those of the deeper-living forms, but with a blue-sensitive cone in addition, absorbing maximally at around 430 nm. The presence of three as opposed to two cone types, covering a wider range of the spectrum, presumably correlates with the wider spectrum of light available to them.

5. **Fishes inhabiting very shallow fresh waters or marine tide pools** also usually have three cone pigments, but compared with group 4, above, the "green" and "red" cone pigments are shifted towards short wavelengths and are comparable in their spectral positions to the cones of terrestrial animals. The light environment in very shallow water is of course similar to that of terrestrial animals, since the filtering effect of the water will be small.

6. A number of species have cones sensitive in the **ultraviolet** range, with an absorption maximum that lies around 355-360 nm. Ultraviolet light is heavily absorbed by water, present at any intensity only in the surface layers, and in some species ultraviolet sensitivity correlates with living near the surface. It is not known what use fish make of their ultraviolet sensitivity.