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8. Adaptation of Visual Pigments to the Aquatic Environment

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8.1 Introduction

A central theme of John Lythgoe's book "The Ecology of Vision" (Lythgoe, 1979) was that of adaptation: the matching between an organism's phenotype and its natural environment. In "The Ecology of Vision", numerous adaptations of animal visual systems were identified, covering diverse aspects of life related to vision including ocular anatomy, visual physiology, biochemistry, behaviour, diet and life style. In this process various striking correlations between the ecology of different species and aspects of their visual systems were described. One of the strongest themes of the book is that of the matching of photoreceptor spectral sensitivities to the visual environment, a theme that was illustrated by numerous examples giving many insights into the evolutionary pressures on visual systems. Indeed, much of "The Ecology of Vision" is concerned with the way in which evolution has driven different species to have the diverse spectral sensitivities that they have today. Nevertheless, the future of the ecology of vision lies in understanding visual adaptations by studies that explicitly identify the selective pressures acting on visual systems.

The theme of visual pigment adaptation in aquatic animals will be the basis of this chapter. John Lythgoe approached this subject by emphasising correlations between the visual pigments of animals and their ecology, and a limited number of such examples are described in Sections 8.8 and 8.9. For a number of reasons, it is important to appreciate the problems inherent in this approach and to realise that it is best at identifying *questions* rather than supplying *answers*. The first and fundamental reason for this is that, from a neo-Darwinian perspective, adaptations are linked to reproductive success; adaptive traits leading to a greater genetic legacy for

an individual. Therefore, to fully assess the adaptive significance of some feature of an animal, one therefore needs to measure the capacity of the adaptation to promote both viability (e.g. growth, foraging ability, longevity etc.) and reproductive success. Such measurements are rarely attempted (but see Endler, 1986, 1987, 1991). Secondly, the uncritical interpretation of supposedly adaptive features presents the danger of *properties* being mistaken for function and being given undue importance. Visual ecologists must be careful that the visual property selected for any 'adaptive' correlation is actually under significant evolutionary pressure for visual tasks, and is not simply a feature that is correlated with some other property of the visual system. Animals function as the sum of their parts and any given adaptation will never function in isolation from other adaptations, or be unconstrained by physical limitations (see Chapter 1). Furthermore, we must keep in mind the phylogenetic history of the trait, and be aware that the visual properties we are investigating are not merely a function of some historic genetic constraint (Harvey and Pagel, 1991). Once appropriate visual properties have been identified, and proper phylogenetic comparisons made, another persistent problem that adaptive investigations must face is that the identification of correlations between supposedly adaptive features (e.g. visual pigment spectral sensitivities) and environmental variables (e.g. spectral irradiance) will inevitably be based on "noisy" data. No two species ever live in the same place, at the same time, and in exactly the same way, so the selective pressures operating on them are never identical. Thus, the interpretation of visual adaptation needs specific knowledge of animals' visual ecology, without which generalisations can well be spurious. Lastly, it is a mistake to assume that a putative adaptation should be perfect: natural selection moulds adaptations to a certain level of effectiveness, which may be a far cry from perfection. Sensory systems are, however, generally acknowledged to be under high selective pressure and, therefore, apparent correlations between some aspect of a visual system and some variable of its operating environment are likely, at least, to provide interesting questions (Endler, 1991; Endler and Théry, 1996; Marchetti, 1993; Fleishman, 1992). This chapter will focus on ways in which visual systems operate in the aquatic environment which, we hope, may suggest avenues for further research in the ecology of vision.

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8.2 Light underwater

The electromagnetic (EM) spectrum covers radiation with frequencies ranging from 10^3 to 10^{22} Hz (Campbell and Dwek, 1984) but only a tiny fraction, known as light, with frequencies between approximately $7.5x10^{14}$ and $4.3x10^{14}$ Hz (corresponding to wavelengths between 400 nm and 700 nm) is visible to humans. In fact, humans can see EM radiation outside this range provided it is of high enough intensity and, when animal vision is considered, it is useful to redefine "light" as that part of the EM spectrum used by all animals, this covering the range from the ultraviolet (UV) to the far-red, with wavelengths (in a vacuum) of approximately 300 nm to 800 nm. Most light originates from the sun but the spectrum of light arriving at the earth's surface is greatly modified by its passage through the atmosphere in ways which vary greatly with latitude, season, time of day, cloud cover etc. (Henderson, 1970; Gates, 1980; Kirk, 1994).

The spectrum of light available at the earth's surface varies considerably throughout the day. When expressed in irradiance units of photons s^{-1} nm^{-1} m^{-2}, (photon units being appropriate for the consideration of visual systems which are essentially photon counters rather than cells that measure energy; Dartnall, 1975), the spectrum of light varies from a predominance of longwave photons during much of the day, to a predominance of shortwave and longwave photons (and dearth of mid-wave photons) at sunset (Henderson, 1970; Munz and McFarland, 1973; McFarland and Munz, 1976). Because of the phenomenon of colour constancy (Pokorny *et al.*, 1991) the magnitude of diurnal spectral change is rarely appreciated by the human observer. Also, because the fraction of light reflected from the water surface is wavelength dependent and is greatly affected by solar angle, the spectrum of light even immediately under the surface can be radically different from that above, especially at sunrise and sunset (Munz and McFarland, 1973; Munz and McFarland, 1977; for review see also Loew and McFarland, 1990). For these reasons it is not easy to calculate the irradiance spectrum at depth from measurements of above surface light, even if diffuse attenuation coefficients (e.g. Jerlov, 1976) are well known. Measurements of spectral irradiance at depth are, however, difficult to make and relatively few data are available (but see Jerlov, 1976; and Kirk, 1994) and for this

reason calculation of underwater spectral irradiance must often be attempted. Such calculations may be based directly on measured spectral diffuse attenuation coefficients (Jerlov, 1976), but Baker and Smith (1982) and Prieur and Sathyendranath (1981) have developed models which can be used to calculate these coefficients from measurements of the concentrations of dissolved organic matter (DOM) and chlorophyll. Such calculations demonstrate that the spectral filtering of light constitutes a major constraint on the light available for vision and not only is the total photon flux rapidly reduced as depth increases, but also the light is quickly restricted in spectral range.

Light underwater is absorbed and scattered in a manner essentially similar to atmospheric attenuation, but with visually significant effects over a few meters path length (Duntley, 1962,1963). This attenuation is strongly dependent on wavelength due to spectral absorption and spectral scattering by: (1) water molecules; (2) chlorophyll in phytoplankton; (3) DOM; and (4) suspended solids. Because the concentrations of 2, 3 and 4 vary widely in different fresh and marine waters, there is wide variation in spectral irradiance at different depths in different waters. Pure water transmits light best at wavelengths close to 460 nm (Morel, 1974; Tyler and Smith, 1970; Jerlov, 1976) and for this reason oligotrophic waters, whether fresh or saline, appear blue. In coastal waters where phytoplankton and run-off from land increases the levels of chlorophyll, DOM, and organic and terrigenous particles, water colour is usually green or yellow. Levels of chlorophyll, DOM and suspended solids vary dramatically within short periods in most inshore waters and plankton blooms and variations in run-off cause unpredictable and extreme variations in spectral transmissions, and hence in the light available for vision. Freshwater is similarly changeable and can vary from extremely clear to green, yellow or brown, although some freshwaters such as Scottish tarns are so heavily stained with DOM that red light penetrates best (Spence *et al*., 1971) and in the blackwater tributaries of the Amazon far-red or even infra red wavelengths predominate (Muntz, 1978; Muntz and Mouat, 1984). Because of the extreme effect of filtering on the spectrum of light available for vision underwater, and the great variability in this spectral filtering in different waters, the study of the evolution of visual spectral sensitivity of animals living in different waters can be thought of as using the underwater environment as a

"natural laboratory" (Levine, 1982). Nevertheless, to fully understand the data provided from this natural laboratory it is necessary to exactly identify the selective pressures that the underwater light environment imposes on visual systems.

For botanists interested in ascertaining the light available for photosynthesis spectral irradiance at depth can be an adequate measure. For visual ecologists, however, this is rarely sufficient because eyes *image* light with optical structures and thus the *direction* at which the light arrives is of fundamental importance. For this reason the vision ecologist is forced to consider the spectrum of light flux from all directions surrounding an aquatic animal, the three dimensional spectral radiance distribution, which is both complex in structure and difficult to measure. Close to the water surface the spectral radiance distribution is particularly complicated, the entire above surface scene being viewed through a cone, with a solid angle of some 97°, known as Snell's window (Jerlov, 1976; Smith, 1974). When an animal looks upwards towards the water surface Snell's window is seen surrounded by light originating from deeper water that is reflected by the water surface (Lythgoe, 1979; Partridge, 1990). The edge of Snell's window, which may be highly distorted by surface ripples and waves, is marked by a narrow ring of different hues where light from the above water horizon is split into a spectrum due to the way in which the refractive index of water varies with wavelength (see Partridge, 1990). Near the surface the 3-dimensional spectral radiance distribution is highly asymmetric, with a marked drop in intensity at the edge of Snell's window and strong shadows cast by the sun (Smith, 1974; Partridge, 1990). However, as depth increases in open water the spectral radiance rapidly approaches an asymptotic distribution that is symmetrical about the vertical axis (Jerlov, 1976). In contrast, the spectral radiance distribution in shallow water, and close to the bottom or other underwater surfaces, is highly asymmetrical. In such habitats the ambient light thus varies markedly in both intensity and spectral composition depending on direction of view (Munz and McFarland, 1977; Levine and MacNichol, 1979, 1982). Typically, the radiance of shallow water substrates is similar in spectral distribution to downwelling light and is spectrally broader than light originating from open water and viewed horizontally (Munz and McFarland, 1977; Levine and MacNichol, 1982).

Given the potential complexity of the light field underwater it is perhaps surprising that a mathematical framework exists for the description of radiance underwater (e.g. Duntley, 1962, 1963; Preisendorfer, 1964) and has been used successfully as a basis for the understanding of vision underwater in both man and fishes (e.g. Lythgoe, 1968; Lythgoe and Partridge, 1991). At heart the radiance transfer equations emphasise the way in which image-forming light reflected from an underwater object is attenuated by absorption and scattering on its passage to an observer, and how this light is "veiled" by a "coloured fog" of light that is scattered into the light path. Figure 1 shows how an underwater visual situation can be reduced to a mathematical description of radiance transfer. In this example, light incident on a small area of a target, (fish 2), originating from all directions surrounding fish 2, but primarily from above, is reflected towards an observing animal (fish 1), which is at a horizontal distance z. This spectral radiance, $R(\lambda)$, which has units of photons s^{-1} m^{-2} nm^{-1} $steradian^{-1}$, is attenuated by absorption and scattering such that the image forming light reaching fish 1 is reduced. This light is also supplemented by non-image-forming "veiling" light that is scattered into the visual pathway and which reduces the contrast between light from target fish 2, ${}_tR(\lambda,z)$, and that of the background spacelight, ${}_bR(\lambda)$. The apparent radiance, ${}_tR(\lambda,z)$, of fish 2 seen at horizontal distance z, is given by an equation that depends on the narrow beam spectral attenuation coefficient, $\alpha(\lambda)$:

$$ {}_tR(\lambda,z) = R(\lambda)e^{-\alpha(\lambda,z)} + {}_bR(\lambda)(1-e^{-\alpha(\lambda,z)}) \qquad [1] $$

The effect of the veiling light is to degrade the contrast of the image in much the same way as atmospheric fog degrades contrast in the terrestrial environment. This has important implications because most visual detection tasks underwater can be reduced to a problem of contrast detection; objects often having inherently low visual contrasts. Because of this fact, and the difficulty that this presents for even the simplest visual task, *a priori* one would expect aquatic animals to have adaptations to their visual systems that would enhance their operational abilities in conditions of low inherent contrast. Contrast is conventionally defined as the proportional difference between the target radiance and the background radiance (Duntley, 1963). In the scenario depicted in Figure 1 the apparent "whole body" contrast, $C(\lambda,z)$, at a

particular wavelength, λ, between fish 2 and the background light at fish 1 is:

$$C(\lambda,z) = ({}_tR(\lambda,z) - {}_bR(\lambda)) / {}_bR(\lambda) \quad [2]$$

This definition of contrast, which has values ranging from -1 to infinity, is similar to a Weber-Fechner fraction (Wyszecki and Stiles, 1967) and can thus readily be related to just detectable contrast differences (e.g. Lythgoe and Northmore, 1973). It is evident that contrast is highly dependent on the visual range and if C(λ,0) is the inherent contrast of the target against the background (i.e. the contrast when the sighting range, z, is zero) then the apparent contrast at horizontal visual range z is:

$$C(\lambda,z) = C(\lambda,0)e^{-\alpha(\lambda,z)} \quad [3]$$

This measure of contrast is relevant for animals engaged in the detection of targets, such as whole organisms (as shown in Figure 1), against the background spacelight. For some visual tasks, however, the background is not spacelight but a substrate such as the sea floor, or even the water surface. A particularly important set of visual tasks are those associated with mate selection and courtship or other social communication and in these cases the background may be part of the animal itself, the target being a specific region of colour on the animal. With such types of visual task, the specific colour contrasts may be compared with the rest of the animal (Endler, 1986, 1991; Endler and Théry, 1996). The relevant measure of contrast in these circumstances may be termed "within body contrast" and can be calculated as:

$$C'(\lambda,z) = ({}_{t1}R(\lambda,z) - {}_{t2}R(\lambda,z)) / ({}_{t1}R(\lambda,z) + {}_{t2}R(\lambda,z)) \quad [4]$$

In this equation target spectral radiance of one body area, ${}_{t1}R(\lambda,z)$, presents a contrast with the spectral radiance of another body area, ${}_{t2}R(\lambda,z)$. In this case the calculated contrast is the difference between the two radiances normalised to the sum of the two radiances, a measure that has somewhat different properties from whole body contrast given in equation (2), and ranges between -1 and +1.

Both whole body contrast and within body contrast will vary depending on the spectrum of the incident light, the viewing distance, the spectral attenuation of the water, and the spectral reflection of the objects being viewed. Aquatic animals, therefore, are likely to be under direct selection for the possession of both effective detecting systems, including retinal and photoreceptor adaptations, and for the use of readily detectable signals such as colour patterns or behaviour that best transmit information within signal degrading environments. In aquatic environments where images are easily degraded, *a priori* reasoning suggests that maximising contrast, both in production and perception, will be a common theme. Such contrasts may be calculated using radiance transfer mathematics but the future importance of this approach in the understanding of aquatic vision will, without doubt, depend on the identification of visual tasks that are essential to an animal's survival and reproductive success. Because such tasks will depend on the behaviour and ecology of the species being considered the successful identification of these tasks will depend on the ethological interpretations of visual behaviour monitored by direct underwater observation and the assessment of these behaviours in terms of their effect on fitness.

8.3 Spectral reflections and the measurement of target radiance

The consideration of radiance transfer in the context of visual tasks of the type shown in Figure 1 underlines an important point about visual systems: they have evolved to look at *things*, rather than to look at the general light field. In the terrestrial world such a statement would seem trite: we are so used to living in a relatively complicated incident spectral radiance distribution and most visual tasks do not involve contrasts between objects and a background spacelight. In some terrestrial habitats, such as forests, the complexity of the incident spectral radiance distribution is very obvious (Endler, 1993) and has a profound effect on the spectral radiance of viewed objects. Underwater, however, the inherent spectral radiance distribution is, in open water especially, dominated by the underwater spacelight, rather than by the spectral reflections of objects in the environment. (see Section 8.2). Consequently, underwater vision ecologists have traditionally concentrated on the optical properties of the water rather than the ethology of vision. Thus, for instance, correlations have

been sought (and found, see Section 8.7) between the spectrum of irradiance at depth and the spectral sensitivities of aquatic animals, often without full consideration of the way in which this is evolutionary significant. Irradiance is a measure of light arriving at a point, either from all directions in the case of scalar irradiance, but also as (e.g.) downwelling, or upwelling vector irradiance. No animal is interested in this *per se* and, instead, the significance of spectral irradiance measurements is that they are a simple measure of the light potentially available for vision. Nevertheless, it is not straightforward to predict the spectral radiance of an underwater target from some measure such as spectral downwelling irradiance because targets are physical objects with particular textures and particular orientation in an underwater light field that is more complex than simple irradiance measurements would suggest (e.g. see Jerlov, 1976). Target radiance is a function of the reflecting properties of the target and the light environment within which it is viewed. Ideally, measurements of the 3-dimensional spectral radiance distribution are required: a Herculean task, and even armed with such data, the calculation of spectral radiance from a target of known spectral reflection is far from straightforward. For this reason there is considerable merit in the direct measurement of spectral radiances from objects in the natural environment.

When *in situ* spectral radiance measurements are not possible, then it is necessary to calculate target spectral radiance from measurements of spectral irradiance, target spectral reflections, and attenuation properties of the viewing medium (e.g. Lythgoe, 1966, 1968; Endler, 1990; Lythgoe and Partridge, 1991). Spectral reflections are an important measurement in the determination of target radiance, and one that cannot be assessed by human eyes alone. The use of spectral reflection measurements based on human perception, even relatively quantitative ones such as those provided by colour comparisons with Munsell chips (Munsell, 1976), are simply not appropriate. Comparisons conducted in this way *may* yield data relevant to the vision of the species under consideration; or they may not. The usefulness of human colour assessment for visual adaptation studies depends on the similarity of the species' visual system to that of the human observer. This argument has been made persuasively by Bennett, Cuthill and Norris (1994) and by Cuthill and Bennett (1993) who have likened the use of human vision in the evaluation of animal visual systems

to the use of human hearing in the understanding of bat echo location. This comparison is valid: just as we are unaware of bat ultra-sound, so we are unaware of hues and even entire parts of the EM spectrum that may be visually accessible to other species. For instance, animal reflections have UV components that we do not see: some tropical marine fish have blue and yellow reflections without a UV component, others have blue and yellows that are also strongly UV reflecting (N. Justin Marshall, pers. com.). To a fish with UV vision the perceived hues of these different blue or yellow patches may look completely different although they look identical to us.

Because of the limitations of human colour vision, the way in which visualised objects reflect light needs to be objectively quantified by reflection spectrophotometry using a reflection system in which the orientation of the object relative to the directions of the measuring device and the illumination source is carefully controlled. Ideally, the illuminating system should emulate the underwater radiance distribution but for practical reasons this is rarely attempted (but see Denton and Rowe, 1994). Indeed, if the animal is subject to variable light conditions, it is useful to make spectral reflection measurements with a full spectrum light source rather than one that emulates only one specific underwater habitat. These types of reflection measurements provide relative reflection spectra which can be integrated with spectral irradiance measurements to produce first approximations of target radiance under various spectral irradiance and transmission conditions.

8.4 Photoreceptors

The scenario depicted in Figure 1 presents a representation of a visual task reduced to the fundamentals of radiance transfer. To utilise such an approach to understand the adaptation of visual pigments to visual tasks demands the incorporation of the process of photon capture by visual pigments located in photoreceptors. In order to function, a visual system needs its photoreceptors to catch adequate numbers of photons to support the visual tasks in which the animal is engaged. In direct sunlight the irradiance in the animal visible spectrum is extraordinarily high, but many animals, particularly aquatic species, never experience high light levels of full sunlight because

the environment in which they live attenuates the available light. Furthermore, even species that sometimes experience full sunlight spend most of their lives at lower light intensities due to atmospheric attenuation and diurnal variations. At wavelengths around 500 nm (i.e. in the middle of animal visible spectrum) full sunlight has an intensity of about $3x10^{16}$ photons s^{-1} nm^{-1} m^{-2} (McFarland and Munz, 1975a), but at twilight this has fallen by three orders of magnitude, and starlight less than 10^7 photons s^{-1} nm^{-1} m^{-2} (Munz and McFarland, 1973). Similarly, full sunlight at 1000 m depth in the clearest tropical oceans is attenuated to approximately 10^8 photons s^{-1} nm^{-1} m^{-2} (Dusenbery, 1992).

The brightness of the retinal image depends largely on the optical construction of an eye (Land, 1981, 1990) but there are constraints on eye design (especially maximum size) that cannot be overcome to increase photon catch. As a result, the main visual problem associated with many visual tasks, even those undertaken in daylight (Land, 1981), is to catch sufficient photons. Both the emission and absorption of photons are stochastic processes and, as a result, the detection of photons and the visual detection of objects in the environment are, at root, statistical problems (Rose, 1973) and the amount of information in a retinal image is fundamentally limited by the number of photons that form it (Buschbaum, 1981). When photon flux is especially low there is no alternative but to increase either the area of the retina over which photon catch is pooled (at the expense of spatial resolution) or to increase the integration time (at the expense of temporal resolution). Both measures will increase the signal to noise (S/N) ratio of the image and the ability of an animal to visually detect large and slow moving objects but the functional significance of this depends on the animal's visual ecology and the visual tasks that it must undertake in order to survive. Alternatively, animals may increase the amount of visual pigment in a photoreceptor to enhance the cell's efficiency at catching photons, most obviously by increasing the size of the photoreceptor. However, this itself has penalties: firstly, a large photoreceptor may be more energetically expensive, or structurally difficult to maintain; secondly, spurious signals from spontaneously "activated" visual pigments, or other sources of receptor noise, will increase with photoreceptor volume; and, thirdly, long photoreceptors conflict with a fundamental requirement for colour vision, the need for adequate separation of spectral sensitivity of different photoreceptor classes.

Visual pigments are membrane bound proteins and are situated in specialised photoreceptors in which many membranes are arranged into compact stacks. The density of packing of rhodopsin in vertebrate rods is about 20,000 molecules μm^{-2} of membrane (Krebs and Kühn, 1977) and the fraction of photons absorbed (i.e. the absorptance; P) of a membrane stack of N membranes is, at the wavelength of peak absorption (λ_{max}), given by Dusenbery (1992) as:

$$P_{\lambda_{max}} = 1\text{-}10^{-0.00013N} \qquad [5]$$

Thus a single membrane absorbs only 0.0003 (i.e. 0.03%) of the incoming photons, even when they have a wavelength at which the rhodopsin is most sensitive. For this reason a visual photoreceptor needs many membranes if its sensitivity is to be adequate for any realistic visual task. In vertebrate rod outer segments membrane discs are separated by approximately 30 nm (Knowles and Dartnall, 1977) and there is therefore effectively one membrane per 15 nm, or about 70 membranes per micrometer of outer segment length. A 1μm length of such an outer segment would thus absorb approximately 0.02 of the incoming photons if they had a wavelength equal to the visual pigment's λ_{max} (i.e. the stack would have an absorbance at the λ_{max} of *ca*. 0.0091). Correspondingly, a 10 μm long outer segment, which is not atypical of rods or cones of shallow living fish (Ali and Anctil, 1976), would absorb approximately 0.19 of the incoming photons (an absorbance of 0.091), and a 100 μm long outer segment (common in deep-sea fish retinas) would absorb approximately 0.88 of the incoming photons, at the λ_{max} (an absorbance of 0.91).

The above calculations disguise the fact that as the length of the outer segment increases the absorptance spectra of photoreceptors become broader, conferring greater sensitivity at all wavelengths, but particularly at those away from the λ_{max} (Knowles and Dartnall, 1977). This broadening of spectral sensitivity also has consequences for the number of different types of photoreceptor that an animal is likely to have because, on theoretical grounds, the number of photoreceptor types that animals "should" have is intimately linked to the spectral bandwidth of the photoreceptors' absorptance spectra. Simply put, an animal's ability to discriminate

radiance spectra from each other will not necessarily be improved by the addition of extra photoreceptors with different spectral sensitivities unless those spectral sensitivities are relatively narrow compared with the extent of the spectrum covered. Barlow (1982) has argued that for sinusoidally modulated ("comb filtered") spectral radiance distributions the possession of three types of visual pigment is probably the optimum solution unless the visible spectrum is extended beyond the human visible wavelengths or the photoreceptors' absorptance spectra are considerably narrowed by intracellular filters (see Douglas and Marshall, in press). Although this conclusion was derived from the consideration of artificial comb filtered spectra similar conclusions have been reached by others (see Osorio and Vorobyev, 1997) with the consideration of additional factors including the spectral reflections of natural objects and the need for colour constancy in colour vision systems.

In the photon limited underwater world there results a particularly acute conflict between sensitivity and the type of colour vision an animal can have. Most fish have more than one type of photoreceptor in their retina: almost all having duplex retinas boasting both rods and cones, and usually several types of the latter (Ali and Anctil, 1976; Bowmaker 1995). In general, rods function at low light levels and cones at higher light levels and fish have complex mechanisms for sensory adaptation to different irradiances, including diurnal retino-motor movements of rods and cones to bring the active photoreceptors into play (Wagner, 1990). All fish with more than one type of cone seem to have the retinal neural machinery to compare the signals from the different cone types, giving the ability to distinguish spectral radiances not just by intensity but also in terms of their spectral composition - i.e. they have the potential for colour vision. For colour vision more than one type of photoreceptor with different spectral sensitivities are required. However, as discussed above, the amount of colour information that can be extracted from a visual scene is limited if the spectral range of environmental light is relatively restricted (Bowmaker, 1983) and the photoreceptor spectral sensitivities are not narrowed by photostable filters (see Douglas and Marshall, in press). In fish, intracellular spectral filtering is relatively undeveloped and, although cone inner segments may in some cases have significant filtering (MacNichol *et al*., 1978), in most species photoreceptor spectral sensitivities are largely determined by the absorptance spectra of the cells' visual pigments. For

this reason it is not surprising that there is good evidence that the number of photoreceptor types present in the retina of different fishes correlates with the spectral bandwidth of the available downwelling light, with the number of spectrally distinct cone types ranging from one to five. For instance, temperate coastal marine fishes living at moderate depths, and experiencing a restricted spectrum of light, have less shortwave and less longwave sensitivity and fewer cone types than tide-pool species living in very shallow water in the same area which experience the full spectrum of daylight (Loew and Lythgoe, 1978; Lythgoe, 1984; Partridge, 1986, 1990). Typically, temperate coastal marine fishes have relatively few types of cones, usually two, with relatively large outer segments and λ_{max} values close to 460 nm and 530 nm (Partridge, 1986, 1990; Lythgoe, 1988; Lythgoe and Partridge, 1991).

For the reasons given above, polychromatic colour vision systems are most likely to be found in shallow living aquatic animals that are exposed to relatively high light levels with a broad spectral range. Indeed, shallow living freshwater fishes generally have at least three types of retinal cone (Levine and MacNichol, 1979; Lythgoe, 1988). Nevertheless, we cannot be sure how the number of photoreceptor types is related to the number of dimensions of an animal's colour vision (Jacobs, 1981). Thus, for instance, we cannot assume that a guppy, which has at least four types of cone (Archer *et al.*, 1987), has tetrachromatic colour vision. Indeed, there may be plasticity in colour vision and the processing of the output from different photoreceptors. For instance, the goldfish, which has four types of cone, has been shown to be tetrachromatic at high light levels but trichromatic when the level of illumination is reduced (Neumeyer, 1992).

8.5 Photoreceptor spectral sensitivity

Photoreceptors of the visual system absorb electromagnetic radiation and amplify the energy content of the arriving photons by the transduction of this photon signal into an ion flow across cell membranes and, ultimately, give rise to a biologically relevant output in the form of neurotransmitter release at a synapse. In this way information about the visual environment is transferred to the internal, physiological environment

of an animal's nervous system. The information capacity of visual systems, especially those of vertebrates, is extraordinarily high and the human eye is capable of transferring information to the brain at rates equivalent to 10^6 to 10^8 bits s^{-1} (Dusenbery, 1992) but such rates of information transfer can only be attained if photon capture itself is efficient.

In all photoreceptors involved in vision it is the absorption of light by coloured compounds, the visual pigments, that initiates the transduction process in the photoreceptor and constitutes the first step in the visual process. Fundamental to this is the successful absorption of photons: only those absorbed by visual pigments can play any part in vision and no amount of subsequent neural processing can replace the information lost when photons are not absorbed (for recent review of photoreceptor spectral sensitivity, see Loew, 1995). The absorption of photons is, however, a stochastic process and the ability of a photoreceptor to signal the arrival of a photon is largely determined by the probability of that photon being absorbed. This probability is a function of the frequency of the photon and the probability of photon absorption varies greatly across the spectrum. Arguably spectral absorptions should be presented as a function of frequency (which is a fundamental property of a photon) but this is rarely done. Instead, visual pigment absorption spectra are generally presented as a function of wavelength, tacitly assumed to be that of the photon in a vacuum despite the fact that wavelength varies with the speed of light (and hence the refractive index of the transmitting medium). In this format, all visual pigments have a major (α-band) absorption peak, the absorbance spectrum of which is asymmetrical and bell-shaped with a wavelength of peak absorbance known as the λ_{max}, at which the pigment is most effective at absorbing photons. If intracellular spectral filters (see Douglas and Marshall, in press) are ignored, the way in which a photoreceptor cell responds to arriving photons of different frequencies is almost entirely determined by the spectral absorptance of the visual pigment that it contains. Spectral absorptance is, itself, dependent on both the spectral specific absorbance (i.e. absorbance μm^{-1}) of the visual pigment and the path length (effectively the photoreceptor outersegment length) presented to the incoming photons (Knowles and Dartnall, 1977). Most available evidence suggests that the spectral sensitivity of a photoreceptor, i.e. the way in which it responds to incident photons of different frequencies, is directly

proportional to its spectral absorptance over much of its sensitivity spectrum (Dartnall, 1972). For the above reasons, much of the investigation of the adaptation of photoreceptor spectral sensitivity to animals' ecology involves the measurement of visual pigment absorbance spectra. Such measurements may be made by spectrophotometry of detergent extracts of visual pigments (e.g. Knowles and Dartnall, 1977; Douglas *et al.*, 1995) or by microspectrophotometry of visual pigments in individual photoreceptor outersegments (e.g. Partridge and DeGrip, 1991).

8.6 Visual pigment λ_{max} and spectral tuning

Fundamental to the appreciation of adaptations in sensory systems is an understanding of the constraints that may be operating on a given system. Such constraints may be due to the physics of the sensory modality, but may also be due to biological limitations operating at all levels from primary protein structure and cell biochemistry to animal behaviour. In the case of the ecology of vision, an understanding of the way in which visual pigments may be adapted to suit specified visual tasks requires knowledge of how such pigments are spectrally 'tuned' and the constraints that may be acting on this tuning.

Visual pigments are the coloured compounds found in photoreceptors, the principle function of which is to absorb light, become "activated" and, in this state, initiate a cascade of intracellular reactions that results in a change in the polarisation of the cell membrane and release of neurotransmitter at a synapse. All visual pigments consist of a chromophore, which is a derivative of vitamin A, and a protein, known as opsin. Vitamin A occurs in two natural forms, A1 and A2, and the aldehydes of these (retinal and 3,4-deyhdroretinal respectively) are both used as chromophores by vertebrates (Knowles and Dartnall, 1977). Invertebrates also use these chromophores, but insects also employ a hydroxylated derivative of retinal, 3-hydroxyretinal (Vogt, 1983), and a few cephalopods use 4-hydroxyretinal in addition to retinal and 3,4 dehydroretinal (Seidou *et al*., 1990) . On their own these compounds absorb most strongly in the near UV, retinal having a λ_{max} close to 377 nm (in solution in ethanol; Knowles and

Dartnall, 1977), and 3,4-dehydroretinal, which has an extra double bond in the terminal ring of the molecule, having a λ_{max} at about 400 nm. These absorption properties are not visually important, however, because the absorption spectrum of the chromophore is radically altered when combined with an opsin to form a visual pigment.

Opsins are transmembrane proteins with seven alpha helices of mainly hydrophobic amino acids (Hargrave *et al.*, 1984). Opsins belong to a large family of cell receptor proteins collectively known as G-protein linked cell membrane receptors, which includes β-adrenergic receptors, muscarinic acetyl choline receptors, dopamine receptors and others. These receptors clearly arose by diversification from a common ancestral protein and are highly conserved in their primary, secondary and tertiary structure, although modified for radically different purposes and signalling intracellularly via somewhat different G-protein mediated mechanisms. All opsins comprise some 350 amino acids, the amino terminal of the protein being exposed on the external surface of the cell membrane (the luminal surface of the outersegment disks of vertebrate rod photoreceptors), and the carboxyl terminal being on the internal cytoplasmic surface (Hargrave *et al.*, 1984). Each α-helix consists of approximately 26 amino acids with a central 18 or so embedded in the membrane (Baldwin, 1993; Schertler *et al*., 1993). Within the palisade of seven α-helices is a ligand binding pocket for retinal, which is bound to the protein via a Schiff base linkage to a lysine residue in helix VII. Like virtually all proteins, opsin absorbs maximally at wavelengths below 300 nm but the electrostatic interaction between the opsin and the chromophore shifts the λ_{max} of the latter to other wavelengths in the electromagnetic spectrum. The exact location of the resulting visual pigment's λ_{max} depends on both the chromophore employed and the amino acid sequence of particular opsins but, in fish, which have the widest spread of λ_{max} values among the vertebrates, the range extends from *ca*. 350 nm to 635 nm. Thus the λ_{max} of the chromophore can be displaced by this 'opsin shift' to either shorter wavelengths (a hypsochromatic shift) or to longer wavelengths (a bathochromatic shift) compared with the free chromophore. If the λ_{max} of a visual pigment is displaced to longer wavelengths this implies that there is a smaller energy difference between the ground and excited states of the molecule (Campbell and Dwek, 1984) and thus low energy,

longwave photons are more likely to be absorbed than photons with shorter wavelengths. In the case of longwave absorbing visual pigments the interaction between opsin and the chromophore must result in an increase in the delocalisation of the chromophore's π electrons. In practice this is achieved by charged and polar amino acids positioned in the transmembrane helices of opsin and particularly by such replacements at sites on the inner surfaces of the helix palisade positioned close to the chromophore. There have been numerous studies of the way in which the λ_{max} values of different visual pigments are spectrally 'tuned' by this interaction and work is particularly advanced in the case of vertebrate cones (see Bowmaker and Hunt, in press) in which various key amino acids involved in λ_{max} tuning have now been identified.

Nevertheless, a given opsin is capable of forming visual pigments with a variety of chromophores, both natural and unnatural. This property has been utilised to study various biochemical properties of visual pigments but is also used by animals. In particular many aquatic vertebrates, especially freshwater fish and amphibians, use 3,4-dehydroretinal as a chromophore to form 'porphyropsin' pigments in their rods and cones, whereas most marine species use retinal to form 'rhodopsins' in their photoreceptors. The absorption spectra of visual pigments based on different chromophores differ significantly: a visual pigment based on a given opsin and employing 3,4-dehydroretinal having a λ_{max} bathochromically (i.e. longwave) displaced compared with a visual pigment based on the same opsin but employing retinal. Not only is the λ_{max} shifted to longer wavelengths but also the normalised absorbance spectrum is generally broader (Knowles and Dartnall, 1977). The relationship between the λ_{max} of analogous pairs of such visual pigments (i.e. based on the same opsin, but employing different chromophores) has been investigated by several workers (e.g. Dartnall and Lythgoe, 1965; Whitmore and Bowmaker, 1989) who have proposed simple equations linking the λ_{max} of porphyropsin visual pigments to the λ_{max} of analogous rhodopsins. Various animals exploit the relationship between rhodopsin and porphyropsin λ_{max} and a number of species, particularly fish living in freshwater, shift their visual pigment chromophores between retinal and 3,4-dehydroretinal either seasonally or during development (see Section 8.9). Although the changes in visual pigment λ_{max} and breadth of spectral absorptance that

occur in such cases are well documented, the adaptive features of such shifts are not well understood. For instance, the adaptive value could be related not so much to λ_{max} but to other properties of rhodopsin and porphyropsin pigments such as thermal stability (see Section 8.9, Loew and Archer, in press).

The discussion of the underwater light field (section 8.2) and the spectral reflections of objects (section 8.3) emphasised the fact that the wavelengths available for vision are affected by wavelength dependent functions. In order to calculate how well tuned a given photoreceptor's spectral sensitivity may be to a particular visual task one must integrate the spectral radiance of the arriving light with the spectral absorption of the photoreceptor. In order to do this the fraction of light absorbed by a photoreceptor (i.e. its absorptance) must be calculated for each wavelength considered in the numerical integration. Spectral absorptance calculations require information about the characteristic way in which a visual pigment absorbs light of different wavelengths, most fundamentally given by its normalised absorbance spectrum ($A(\lambda)$; Knowles and Dartnall 1977); the length specific absorbance of the visual pigment (s; i.e. the absorbance per micron of photoreceptor, measured at the λ_{max}); and the total path length (l) presented by that structure to incoming photons (e.g. the length of the outer segment in the case of vertebrate rods and cones). The spectral absorptance ($P(\lambda)$) is thus given by:

$$P(\lambda) = 1\text{-}10^{-A(\lambda)sl} \qquad [6]$$

Although $A(\lambda)$ can be measured by microspectrophotometry of individual photoreceptors (Liebman, 1972; Partridge, 1986; Partridge and De Grip, 1991) or by spectrophotometry of visual pigments extracted in detergent or solvents (Knowles and Dartnall, 1977; Douglas *et al*., 1995) such measurements are not always necessary, particularly in theoretical studies. This is because the normalised absorbance spectrum of a visual pigment of a given λ_{max} is readily calculated by using visual pigment template curves, transformed appropriately on the spectral axis: i.e. visual pigments have a more or less standard normalised absorbance spectrum if the wavelength axis is transformed in an appropriate way. There have been numerous attempts to describe standard normalised absorbance spectra of different classes of

visual pigments (principally those based on different chromophores) and various spectral axis transforms have been suggested (e.g. Dartnall 1953; Partridge and De Grip, 1991; Stavenga *et al.*, 1993). Such templates provide a simple way of calculating the normalised spectral absorbance of visual pigment with a given λ_{max}, but all have limitations: for instance many only consider the principal (α) absorbance band of the visual pigment (Knowles and Dartnall, 1977), although the rhodopsin and porphyropsin templates of Stavenga *et al.* (1993) extend to shortwave β-band and γ-band absorbance. In addition, there are many assumptions underlying the templates: for instance Stavenga *et al*., (1993) assume that the β-band does not shift its spectral location when the α–band λ_{max} is shifted, although others have suggested relationships between these bands (e.g. Palacios *et al.*, 1996). There is also accumulating evidence that visual pigments with very shortwave λ_{max} values, especially UV sensitive pigments have absorbance spectra that are substantially narrower than is predicted by standard templates (e.g. Palacios *et al.*, 1996). Despite such reservations, however, visual pigment templates provide excellent tools for the analysis of visual pigment spectroscopic measurements (e.g. Partridge and De Grip, 1991). Moreover, in the context of the ecology of vision, visual pigment templates are particularly useful when constructing optimisation models of visual pigment function. Such models are essential to develop hypotheses concerning the spectral tuning and adaptive value of visual pigment spectral sensitivities and have considerable predictive potential (e.g. Lythgoe and Partridge, 1989, 1991; Vorobyev and Osorio, 1998).

As previously noted, the range of known visual pigments is large, with peak sensitivities ranging in wavelength from the UV to longwave red. Nevertheless there is evidence that there are limits on the variability of λ_{max} values. Principle among these data is the discontinuous nature of the distribution of λ_{max} values, some values being far more common than others and some apparently never being found. These data have been gathered principally from measurements of aquatic animals, especially fishes, and such spectral "clustering" of λ_{max} values has been demonstrated both for porphyropsins (Bridges, 1964) and for rhodopsins (Dartnall and Lythgoe, 1965; Partridge *et al*., 1989). These data indicate that visual pigment measurements fall into distinct classes with λ_{max} separations of 5-8 nm, individual species having visual

pigments selected, teleologically speaking, from a finite and discontinuous palette of λ_{max} values. As our understanding of the molecular basis for spectral tuning has increased (see Bowmaker and Hunt, in press; Loew and Archer, in press) an explanation for λ_{max} clustering has been presented: only a limited number of amino acids within the opsin molecule can have an effect on π-electron delocalisation; others are simply too remote from the chromophore to have significant influence on a visual pigment's absorption spectrum. It is also likely that there are other molecular constraints on the spectral location of a visual pigment's λ_{max}. In particular, visual pigments must function in ways other than simply absorbing photons: they must be structurally coherent, stable (i.e. only become activated when a photon has been absorbed), and they need to interact efficiently with the other proteins involved in transduction (Piantanida, 1991). It is entirely likely that these requirements impose irreducible constraints on the range of λ_{max} values that functional visual pigments can have.

As knowledge of the molecular biology of visual pigments has increased an explanation for the empirical observation of spectral clustering of λ_{max} values has been presented as particular amino acids in the opsin molecule have been identified as being responsible for discrete shifts in λ_{max} (see Bowmaker and Hunt, in press; Loew and Archer, in press). Such data reinforce the earlier assumption that λ_{max} clustering is driven by physical limitations associated with opsin-chromophore interactions rather than environmental constraints: a conclusion reached simply because all the variables associated with radiance transfer are continuous rather than discrete. Indeed, the discontinuous distribution of λ_{max} values may well represent the limit to which λ_{max} adaptation by opsin evolution can be achieved in response to selective pressure for the spectral tuning. Thus, natural selection does not *cause* the λ_{max} clusters (which are caused by biophysical or biochemical constraints) but natural selection *will* determine the cluster into which a given photoreceptor visual pigment will fall. Given the potential for fine tuning λ_{max} by using a mixture of different chromophores, not to mention the potential for refinement of absorptance spectra by altering the size of photoreceptor outer segments, the discontinuity in λ_{max} due to opsin sequence may not be particularly restrictive in terms of optimisation of spectral

tuning of photoreceptors. Nevertheless, it is likely that the adaptation of λ_{max} in response to selective pressure associated with environmental variables and specific visual tasks cannot be perfect because of the clustering phenomenon.

8.7 Visual pigments of aquatic animals: background

There is now a considerable body of information about the visual pigments of aquatic animals, much of this gleaned from studies inspired by the supposition that the severe limits on the spectrum of light available for vision underwater would be reflected in adaptations of visual sensitivity. Among the invertebrates, most work has centred on the crustacea, species of which have a great diversity of visual pigments, utilising both retinal and 3,4-dehydroretinal as chromophores, and ranging in number from single pigments in many amphibious and deepsea decapods to at least 11 visual pigments in stomatopods (see Marshall, Kent and Cronin, in press). Crustaceans have evolved visual pigments with wavelengths of peak absorbance encompassing UV sensitive rhodopsins to far-red sensitive porphyropsins and, together with great variety in optical design, have possibly the most diverse visual systems of any group (for reviews, see Marshall, Kent and Cronin, in press; and Land, in press). Within the phylum Mollusca the visual pigments of several cephalopods have been measured, principally by extraction of visual pigments (Seidou, 1990), but also by microspectrophotometry (Michinomae *et al.*, 1994), and several species have been found to have multiple visual pigments separated in different types or parts of rhabdoms (Seidou, 1990). Surprisingly, however, there is no evidence for colour vision in any cephalopod (Hanlon and Messenger, 1996; Marshall and Messenger, 1996), despite their obvious and spectacular ability (to a human observer) to modulate their dermal coloration for intraspecific display and crypsis. Most cephalopods utilise retinal as their visual pigment chromophore (Seidou *et al*., 1990) but two species, *Watasenia scintillans* and *Bathyteuthis* sp. also use 3,4-dehydroretinal (Matsui *et al*., 1988; Kito *et al.*, 1992a) and several deepwater species (the squids *Pyroteuthis* sp. and *Pterigioteuthis* sp. and the octopus *Japetella* sp.) also employ 4-hydroxyretinal (Kito *et al.*, 1992a). Visual pigments based on 4-hydroxyretinal (which could be named ‘cephalopsins’ in view of the class of molluscs in which they were first

discovered, although this may be etymologically slovenly) have λ_{max} values at shorter wavelengths than rhodopsin pigments based on the same opsin. For instance the cephalopsin analogue of a rhodopsin having a λ_{max} of 501 nm has a λ_{max} at 486 nm, but otherwise the two classes of pigments have very similar normalised absorbance spectra and very similar extinction coefficients (Kito *et al*., 1992b). All available evidence suggests that the rhodopsin and cephalopsin visual pigments of deep-sea cephalopods have λ_{max} values spectrally tuned to confer high sensitivity at different depths in the open ocean (in *Watasenia scintillans*, for instance the cephalopsin, rhodopsin and porphyropsin pigments have λ_{max} values of 470, 484 and 500 nm respectively; Matsui *et al*., 1988; Seidou *et al*., 1990). Such a range of pigments demonstrates an interesting evolutionary convergence with both deep sea crustaceans (see Marshall, Kent and Cronin, in press) and mesopelagic deep-sea fishes (e.g. Partridge *et al.,* 1988, 1989, 1992) which also have visual pigments with similar λ_{max} values but employing retinal rather than 4-hydroxyretinal as the chromophore.

More work has been conducted on the visual pigments of aquatic vertebrates. Mammals are not a taxon with well developed colour vision and aquatic mammals such as seals and cetaceans have retinae dominated by rods. Little information is available about cone visual pigments in these animals but data on rod visual pigments demonstrates that there is λ_{max} convergence with deep-sea fishes: deeper diving mammals having visual pigments with more shortwave λ_{max} values (Lythgoe, l972a). Few birds have had their visual pigments measured (Bowmaker *et al.*, in press) and the only aquatic, or semi-aquatic species so far investigated are the mallard duck (*Anas platyrhynchos;* Jane and Bowmaker, 1988) and the Huboldt penguin (*Spheniscus humboldti;* Bowmaker and Martin, 1985). No firm conclusions can be made about avian visual pigment adaptations to underwater vision based on such limited data, although there is evidence that diving birds may have different proportions of cone types and oil droplets with cut-off wavelengths different from most birds (Partridge, 1989). Unlike birds and mammals, which only use retinal as a chromophore, aquatic reptiles have evolved both rhodopsin and porphyropsin visual pigments, with the latter being more common, apparently, in freshwater species (e.g. the terrapin *Pseudomys scripta elegans*; Liebman and Granda, 1971). The predominance of porphyropsins in freshwater reptiles is mirrored in amphibians

which, as tadpoles, tend to have predominantly porphyropsins in their retinas, but at metamorphosis and emergence from water, switch more or less to rhodopsins (see Knowles and Dartnall, 1977; Lythgoe, 1979). Species that remain aquatic, such as *Xenopus laevis*, are exceptions to this rule and retain porphyropsins as adults (Crescitelli, 1973; Witkovsky *et al.*, 1981).

Naturally, the most obvious group of vertebrates to study when searching for adaptations of visual pigments to the underwater world are fishes: they have had a long evolutionary history and in that time have radiated into *ca.* 25000 extant species (Nelson, 1994). Fishes occupy an extraordinary range of aquatic habitats that includes near terrestrial visual worlds (e.g. mudskippers such as *Boleophthalmus*) to habitats that never include the water surface (e.g. most deep-sea fish); from lives in hot soda lakes at 44 °C (e.g. *Tilapia* in East Africa) to sub zero temperatures in the Antarctic (e.g. Nototheneid cod ice fish); from high altitude freshwater lakes (e.g. cyprinodontids in Lake Titicaca, 3812 m above sea level) to the extreme depths of the ocean (e.g. species in the Marianas Trench, 11 km deep); from existences in the clearest oceans to lives in highly turbid estuaries and rivers (Nelson, 1994). Much data are available about the visual pigments of both the rods and cones of many hundreds of species of fishes and these data have been regularly and exhaustively reviewed by numerous authors, usually from a tacitly adaptationist perspective (e.g. Lythgoe 1972b, 1979, 1980, 1984; Loew and Lythgoe, 1978; Ali and Wagner, 1975; Crescitelli, *et al*., 1985; McFarland and Munz, 1975b; Munz and McFarland 1973, 1975, 1977; Knowles and Dartnall, 1977; Levine and MacNichol 1979; Bowmaker 1990, 1991a, 1991b, 1995; Partridge, 1990; Douglas, *et al.*, 1995; Partridge *et al.*, 1988, 1989, 1992). In almost all cases these authors have described correlations between the observed visual pigment data and some aspect, or aspects, of the underwater visual environment. In most cases, however, there has been little effort to separate the potentially confusing combination of phylogenetic and ecological information, far less to eliminate this confusion by use of an appropriate statistical method (cf. Harvey and Pagel, 1991).

Nevertheless, two approaches have partly circumvented this problem. The first has been to reduce the potential phylogenetic confusion by concentrating on closely

related, sometimes endemic species. Such studies include the work of Muntz (1976) on Lake Malawi cichlids; that of Bowmaker *et al*., (1994) and Hunt *et al.*, 1996 on Lake Baikal cottoids; and that of Lythgoe *et al.*, 1994) on Great Barrier Reef snappers of the genus *Lutjanus*. The merits of this approach are further discussed in Section 8.8. The second approach is to suggest a hypothesis that defines the "best" visual pigments for certain visual tasks and to construct models, with predictive value, with which the visual pigment data may be compared.

Such models are not new in the context of underwater vision and one of the first, the Sensitivity Hypothesis, simply predicts that, because of the importance of photon capture in any visual task, visual pigments should have λ_{max} values spectrally located to maximise photon catch during adaptively important visual tasks undertaken in the visual environment in which the animal lives. Underwater, the environmental attenuation of light ensures that light levels are often low and catching as many photons as possible is of paramount importance. The eyes of fishes show numerous adaptations towards the maximisation of photon catch including optics designed to give a bright retinal image (Fernald, 1988) and tapeta which reflect light back through the retinal photoreceptors for a "second chance" of being absorbed. For similar reasons a number of fishes, including crepuscular predators (Lythgoe, 1988), but more especially deep-sea fishes (Ali and Anctil, 1976), have evolved particularly large photoreceptors in which the unusually long path-length that light must travel in the outer segments, often as much as 100 μm, substantially increases the chances of photon absorption. Deep-sea fishes have also increased the density of visual pigment in the outer segments (Munk, 1966; Partridge, *et al*., 1989) and specific optical densities may be as high as 0.028 μm^{-1} in these animals (Partridge *et al.,* 1989), very much higher than the range 0.010 μm^{-1} to 0.015 μm^{-1} that is typical of shallow living fishes (MacNichol *et al*., 1973; Knowles and Dartnall, 1977; Partridge, 1986). Given these anatomical adaptations it is surprising that there is very little support for the Sensitivity Hypothesis, except in the case of deep-sea species, and most animals do not have visual pigments, even those subserving vision at scotopic light levels, with λ_{max} values spectrally located to maximise photon catch (Partridge, 1990). One possible reason for this is that "sensitivity" in visual systems is actually best expressed in terms of the signal to noise ratio (S/N) associated with the visual task.

Although S may be increased by spectral tuning of λ_{max} this will only be advantageous if N is increased by a lesser proportion, otherwise S/N may, in fact, decrease. At low light levels the noise, both from the light signal itself (channel, or photon noise) and from the visual system (dark noise), imposes limits on S/N and hence on visual performance. Although visual pigments are extremely stable and rarely signal spontaneously (i.e. without photon absorption) visual pigment molecules are found in retinas in such high numbers that some visually significant spontaneous activity is inevitable. For this reason an animal's ability to detect dim lights is limited by noise in its own visual system, with rhodopsin being, in all probability, the primary noise source (Barlow *et al*., 1993). Indeed, as the volume of an outersegment essentially determines the number of visual pigment molecules present in a photoreceptor, rhodopsin dark noise may well be an important constraint on photoreceptor size. Moreover, if some visual pigments are less susceptible to spontaneous isomerisations than others then there will be selection pressure for these pigments regardless of λ_{max}, especially in photon-limited environments. On thermodynamic grounds visual pigments with longer wavelength λ_{max} values are more susceptible to spontaneous isomerisations due to thermal excitation (Barlow, 1957) and empirical evidence suggests that the most stable visual pigments do indeed have shortwave λ_{max} values (Firsov and Govardovskii, 1990). In photon limited environments noise prone visual pigments will be unacceptable, even if their spectral sensitivities better match the available light than other, less noisy, pigments if their effective S/N is lower.

It is quite possible the evolution of visual pigments for scotopic vision has been driven largely by the need to maximise S/N by the employment of noise-free visual pigments (see Loew and Archer, in press). Nevertheless, an alternative explanation of why visual pigments may not be spectrally located to maximise sensitivity is provided by the Contrast Hypothesis (Lythgoe, 1966, 1968). Most visual tasks involve the detection of changes in light levels, either with time or in space, and the larger the change the easier the task of detection (Land, 1981). Spatial contrasts may be greater in regions of the spectrum where radiances are less than at other wavelengths and in these cases visual pigments with λ_{max} values 'offset' from the wavelengths of greatest light flux may confer advantages in contrast detection tasks. In the context of the

visual task depicted in Figure 1 the contrast between the observed radiance from fish 2 and that of the background can be calculated by computing the photon catch of photoreceptors receiving light from the two sources. The visual pigment that provides the greatest visual contrast (C″) is then given by:

$$C'' = (I_t - I_b)/I_b \quad [7]$$

Where I_t is the photon catch of a photoreceptor in the retina of fish 1 receiving light from target fish 2 and I_b is the catch of a photoreceptor receiving horizontal background spacelight. These photon catches can be approximated as:

$$I_t = \sum_{\lambda=300}^{\lambda=800} P(\lambda)T(\lambda)R_t(\lambda,z) \quad [8]$$

$$I_b = \sum_{\lambda=300}^{\lambda=800} P(\lambda)T(\lambda)R_b(\lambda,z) \quad [9]$$

Where $P(\lambda)$ is the spectral absorptance of the photoreceptors, $T(\lambda)$ is the spectral transmission of intraoccular tissues such as the lens and cornea, and ${}_tR(\lambda)_z$ and ${}_bR(\lambda)$ are spectral radiances from target and background respectively, as shown in Figure 1, although absolute catches require other variables to be taken into account.

Using such methods it can be shown that visual contrasts are often greater for visual pigments with λ_{max} values offset from the wavelengths of maximum irradiance and several authors have discussed the advantages of such 'offset' visual pigments in contrast enhancements (Lythgoe, 1966, 1968, 1979; McFarland and Munz, 1975b; Munz and McFarland, 1977; Levine and MacNichol, 1979; Loew and Lythgoe, 1978). In general, 'offset' visual pigments increase the contrast of light targets seen against a darker background spacelight, but when a dark target is seen against a lighter background a visual pigment most sensitive to I_b will maximise contrast. Once again, however, it is important to appreciate that the contrast signal C″ is subject to noise due to the inherent fluctuations in I_t and I_b due to photon noise. Thus some 'offset' visual pigments may appear to produce a very high contrast but in fact have a photon

capture rate that is so low that the contrast signal is too noisy to be visually useful. Because I_t and I_b follow Poisson distributions the noise associated with these signals can be readily calculated (Land, 1981) and thus the S/N of C″ can be computed (see Lythgoe and Partridge, 1991) *as long as* I_t and I_b have been measured in absolute units (photons s^{-1}) not relative ones (see Roderick1998).

This approach can be extended to consider multiple visual pigments and has been used by Lythgoe and Partridge (1991) to predict the best pairs of rhodopsins for the discrimination of targets on the basis of luminosity and colour contrast ('chromaticity'). The model, which considers dichromats living in green coastal waters, utilises the statistics of photon capture by cones and predicts that a λ_{max} of 535 nm to 560 nm would be best for brightness discriminations, depending on the objects considered and viewing conditions. For 'chromaticity' discriminations the model predicts that a shortwave sensitive cone (λ_{max} *ca*. 440 nm - 470 nm) should be paired with a longer-wave cone having a λ_{max} of approximately 530 nm. The predictions of this model compare well with actual data from temperate coastal fishes which generally have two cone types: a single shortwave sensitive cone with a λ_{max} between 440 nm and 470 nm, and double cones with λ_{max} values between 520 and 540 nm (Lythgoe, 1984; Lythgoe and Partridge, 1991).

8.8 Case Studies

Investigations that seek to understand the ways in which visual systems vary among species living under different optical environments, require that due account be taken of other sources of influence such as phylogenetic constraint and non-environmental sources of selection (e.g. predation avoidance, foraging etc.). In the last decade a few investigations have attempted to control for phylogeny by examining the visual systems of closely related species that live in optically different habitats. Bowmaker *et al*. (1994) conducted a microspectrophotometric survey on an endemic group of 17 Cottoid species in Lake Baikal. Species within this group of fish partition the lake into different habitats, principally by depth range. Thus the most shallow dwelling species (e.g. *Cottus kessleri* and *Paracottus kneri*) live at depths between 1 m and 5

m, whereas the pelagic species (e.g. *Comephorus dybowskii* and *Comephorus baicalensis*) live at various relatively species specific depth ranges between 300 m and 1500m. The total depth range occupied by these fishes is correlated with dramatic changes in optical habitat, from full spectrum sunlight in the shallow regions to dark and nearly homochromatic in the deepest habitats. The results of the survey by Bowmaker and colleagues illustrate that species living at different depths have different sets of visual pigments, this variation appearing to be related to the wavelength of maximum irradiance at different depths. Shallow dwelling species, living in waters with wavelengths of maximum transmission between 550 nm and 600 nm, have double cones with λ_{max} values between 500 nm and 545 nm. As depth increases, the λ_{max} values of the longwave sensitive double cones found in deeper living species shift to shorter wavelengths, between 500 nm and 521 nm, and the wavelength of maximum transmission of the water at such depths shifts to *ca*. 490 nm. A similar shift occurs in the λ_{max} of the single blue cones, with shallow species (e.g. *Cottus kessleri*) having a λ_{max} around 449 nm, whereas in the deeper species (e.g. *Limnocottus griseus*) the blue cone has a λ_{max} close to 431 nm. There is also a shift to shorter wavelengths in rod λ_{max} values of the deeper dwelling species: shallow dwelling cottoids having rod λ_{max} values ranging from 510 - 520 nm whereas abyssal species have rod λ_{max} values between 480 nm and 500 nm.

The assumption underlying the study of closely related species is that they all share a relatively recent common ancestor, and therefore differences observed among the descendants are likely to be driven by different selection pressures that have operated during and since speciation. The factor most likely to be responsible for the changes in visual sensitivity among the Baikal cottoid fishes is the variation in available light at different depths. The shift in the λ_{max} values of the double cones to shorter wavelengths with increasing depth gives credibility to the selective role that the environment has on photoreceptor sensitivity, since the λ_{max} of the double cones is correlated with a shift in wavelength of maximum irradiance of the environment. Such results lends support to the "Sensitivity Hypothesis" which suggests that there is likely to be selection pressure operating on photoreceptors to maximise photon capture (see Section 8.7 and Loew and Archer, in press). The shortwave shift in blue

cone λ_{max} values, however, appears to contradict the predictions of the Sensitivity Hypothesis for two reasons: (1) the light available at these depths is found in the longer wavelength region of the spectrum, and (2) the total amount of light available at these depths is well below known cone threshold levels. Why, therefore, would blue cone λ_{max} values be shifted to a part of the spectrum where there are fewer photons available in the downwelling spectrum, and why bother with cone photoreceptors at all in so dim an environment? These questions suggest that other selection pressures may be involved in the observed shortwave shifts of rod and cone photoreceptor sensitivities with increasing depth. One possible explanation is that shortwave photoreceptors are likely to have less thermally induced noise (see Section 8.7 and Loew and Archer, in press). In visual conditions where the signal to noise (S/N) ratio is under selection for maximisation but where the inherent signal (S) is unavoidably low, such as in deeper regions of Lake Baikal, there may be high selection pressures for photoreceptor sensitivity that maximises S/N by minimising noise (N). Undoubtedly our understanding of this issue would be greatly enhanced by further measurements of the intrinsic noise (Barlow *et al*., 1993) of rod and cone photoreceptors containing visual pigments of different λ_{max}.

The study of the visual pigments of Baikal Cottoids is likely to become a classic in the ecology of vision and is considerably strengthened by the associated work on the molecular biology of Cottoid opsins (Hunt *et al.*, 1996) which explains how the visual pigments of these animals are tuned by opsin sequence. Nevertheless, the species examined are relatively diverse in both their taxonomy and in their visual behaviour. This problem can be overcome, at least partly, by the study of very closely related species that exhibit behavioural similarities and have superficially similar visual tasks while living in habitats with contrasting environmental conditions. This approach was taken by Lythgoe *et al*. (1994) who surveyed the visual pigments of 12 species of snappers (genus *Lutjanus*) living in different optical habitats in the Australian Great Barrier Reef. This study attempts to isolate the effect of the environment on photoreceptor sensitivity by focusing on congeners with similar foraging habits and behaviour. The results show that congeners living in different light environments have divergent visual pigment combinations. Lutjanid species that occupy the outer reef environments, in which the irradiance spectrum is dominated by short

wavelengths (maximum transmission *ca*. 490 nm), have three cone classes with relatively shorter wavelength λ_{max} values (e.g. *L. kasmira* has cone λ_{max} values at 430 nm, 487 nm, and 518 nm). In contrast, Lutjanids living in the more heavily DOM dominated waters of the near-shore estuaries have cones with relatively long wavelength λ_{max} values (e.g. *L. fulviflamma* has cone λ_{max} values at 505 nm, 534 nm, and 568 nm). The study attempted to test the predictions of the Sensitivity Hypothesis by comparing the λ_{max} data with calculations of the λ_{max} of the rhodopsin visual pigment that would confer the greatest sensitivity in each optical habitat. The λ_{max} measurements reveal that all but one of the 12 Lutjanid species have double cone λ_{max} values spectrally positioned such that they would be more than 90% as effective at capturing photons as the most sensitive possible visual pigment.

This spectral location of double cone λ_{max}, tuned to confer high sensitivity to the spectrum of available light, also appears to be the case for temperate coastal marine fish (Lythgoe and Partridge, 1991) as well as the Lake Baikal cottoids. The placement of the λ_{max} values for the blue sensitive photoreceptors, however, is not as simple to understand. Lythgoe *et al.* (1994) calculated rates of photon capture by shortwave sensitive cones for the 12 Lutjanid species and determined their photon capture rates to be only 20% - 40% of that of the other cone types in any given optical habitat. The suggested explanation for this difference is that, whereas the double cones offer sensitivity to the downwelling spectrum, the blue cones may have a greater role in hue discrimination when light is not limiting. How the placement of blue cone λ_{max} is determined by such a putative need for hue discrimination is not well understood, and any attempts to reveal their role will require detailed knowledge of relevant (i.e. adaptively important) visual tasks.

The identification of such visual tasks, particularly those associated with foraging, predator avoidance, and reproductive behaviour will provide information essential to the further understanding of the spectral tuning of λ_{max}. Implicit in such studies is the identification of visual tasks that confer some fitness advantage. The analysis of such tasks in terms of photon capture by photoreceptors will involve measurement of radiance spectra from the visual targets involved in defined visual tasks, and the use of these data in models that consider such issues as how λ_{max} values vary in the

optimisation of sensitivity and contrast (see Sections 8.2 and 8.7). Such data are not easy to obtain, particularly as fitness advantage related to these tasks also needs to be properly quantified, but such an approach is now both timely and essential if further evaluation of the adaptive pressures on visual pigment λ_{max} is to be achieved.

8.9 Visual pigment plasticity

The study of closely related species, such as those detailed above, at least partially eliminates the potentially confusing interaction of phylogeny and ecology in studies focused on the understanding of visual pigment adaptation. Nevertheless, another route offers even greater potential: the study of the adaptive value of visual pigment shifts within individual species. As explained in section 8.6, the λ_{max} of a visual pigment is determined both by the amino acid sequence of its opsin and by the nature of the chromophore employed. Many species of fish exhibit λ_{max} plasticity during their lives, achieving this plasticity both by opsin shift and by chromophore exchange. Often such shifts are correlated with environmental changes, with migration between different photic environments (e.g. catadromous and anadromous species), or with ontogenetic events.

Many species of freshwater teleosts, including the speciose cyprinids, have retinae dominated by porphyropsin visual pigments, but have the potential for the incorporation of rhodopsin pigments. The best studied example is the probably the rudd (*Scardinius erythrophthalmus*) in which both rod and cone visual pigments have been shown to be based on mixtures of retinal and 3,4-dehydroretinal chromophore (Whitmore and Bowmaker, 1989; for review see Bowmaker, 1995). In general wild rudd have retinas dominated by porphyropsins, with rod pigments having λ_{max} values close to 543 nm and longwave cones most sensitive at *ca*. 620 nm, but in summer these shift by chromophore exchange to have λ_{max} values close to 510 nm and 565 nm respectively. The adaptive significance of such shifts is, however, far from clear. Although correlations with seasonal shifts in spectral irradiance in rudd habitats have been noted, the λ_{max} shifts are generally contradictory to the observed irradiance shifts, suggesting that sensitivity maximisation is not the primary selection pressure.

Also, different populations of rudd exhibit different degrees of chromophore shift, and the degree of annual chromophore shift diminishes with increasing age such that older animals have, more or less, only porphyropsin pigments. The explanation most focused on the concept of adaptation to a vital visual task is that of Muntz and Wainwright (1978) who suggest that the rudd's seasonal visual pigment shift may be due to annual changes in feeding strategy since rudd tend to feed closer to the surface in summer than in winter. However, the validity of this suggestion, and its adaptive significance, remains to be tested.

Shifts in rhodopsin:porphyropsin ratios are also found in migratory fishes and, once again, it is tempting to identify environmental correlates with visual pigment sensitivity. One of the best documented is the European eel (*Anguilla anguilla*) which hatches in the Sargasso Sea, and drifts as a leptocephalus larva to the coastline of Europe where it metamorphoses into a glass elver and enters the river systems. At this stage the rod visual pigment shifts from rhodopsin with a λ_{max} close to 502 nm, typical of marine fishes, to a porphyropsin with a λ_{max} close to 523 nm typical of freshwater fish (Wood *et al*., 1992). Eels remain in freshwater as "yellow eels" for several years before migrating downstream, during which time the chromophore exchange is reversed and is accompanied by the expression of a new opsin, giving a rhodopsin pigment with a λ_{max} of 482 nm (Wood and Partridge, 1993). The new pigment essentially gives the now 'silver eel' the retinal sensitivity of a deep-sea fish (Partridge *et al*., 1989) and may, in this case, be an adaptation for visual sensitivity during the deep-water migration across the Atlantic.

The new 'deep-sea' opsin of the eel, which has been sequenced and putative spectral tuning sites identified (Archer *et al*., 1995), has been shown to be incorporated into the outersegments of existing rods (Wood and Partridge, 1993). Thus for some time two different opsins are found in the single photoreceptors. Rod opsin exchange is also reported in the cardinal fish, *Apogon brachygrammus*, (Munz and McFarland, 1973) which, as a larva, has a rhodopsin with a λ_{max} at 482 nm and, as an adult, has a rhodopsin with a λ_{max} of 494 nm. However, it is unknown whether this involves expression of different opsins in the same photoreceptors. In cone photoreceptors such dual expression of opsin genes has been suggested in the longwave sensitive

cones of the guppy (Archer and Lythgoe, 1990) and is also implicated in the shortwave cones of the pollack (*Pollachius pollachius;* Shand *et al.*, 1988). In the latter species, which is a coastal marine gadoid, the duplex retina contains rhodopsin pigments both in its rods (λ_{max} 489 nm) and in its two types of cone pigment. The identical paired cones contain a visual pigment with a λ_{max} at 521 nm, but the single cones contain a shortwave pigment which, in small fish has a λ_{max} close to 410 nm, but in larger fish has a λ_{max} close to 460 nm. The shift in shortwave cone λ_{max} occurs during the development of the fish as they move into deeper water, where there is less shortwave light, and change their diet from mainly plankton to mainly benthic crustaceans. Whether it is the change in light environment *per se*, or the change in diet, and thus visual task, that has led to the evolution of this shortwave cone shift has yet to be determined, but clearly there is potential in such a study.

A similar uncertainty surrounds the adaptive significance of the ontogenetic changes in the visual pigments of the tropical reef goat fish, *Upeneus tragula* (Shand, 1993, 1994) As pelagic, surface living larvae this species has double cones with one member containing a longwave sensitive rhodopsin (λ_{max} 580 nm), and the other containing a relatively shorter-wave sensitive pigment (λ_{max} 487 nm). At metamorphosis to a benthic subadult extensive somatic morphological changes are accompanied by a shift in the longwave cone to a λ_{max} at 530 nm, although the other cone and rod pigments do not appear to shift. Once again, the adaptive advantage of this visual pigment shift may be purely due to environmental factors (there is somewhat less longwave light even at the relatively shallow benthic depths of the metamorphosed animals than are found at the surface) or it may be related to the visual tasks associated with the new mode of life.

Similar ontogenetic shifts in opsin expression are known in a number of other fishes, including salmonids in which the UV sensitive pigments appear to be lost and regained at different phases of life (see Beaudet and Hawryshyn, in press); the temperate pomacentrid *Chromis punctipinnis* (McFarland and Loew, 1994) which has a violet-sensitive cone as a juvenile (λ_{max} 417 nm) but loses this in favour of a UV-sensitive cone as an adult (λ_{max} ca. 350 nm); and the flounder *Pseudopleuronectes americanus* (Evans *et al*., 1993), which has a single cone with at λ_{max} at 519 nm as a

larval fish, but which develops a duplex retina with both rods and cones as an adult, the latter cells expressing three visual pigments with λ_{max} values at 457, 531 nm and 547 nm. Such examples of visual pigment plasticity, exhibited by species with diverse phylogenies, makes it highly likely that many fish will be found to shift their visual pigments at times of development when the nature of their visual tasks change significantly. The proper investigation of such changes is, arguably, the most useful means by which the adaptive advantage of visual pigment sensitivities can be directly investigated.

8.10 Conclusions

The study of visual pigment adaptation in the aquatic environment has been an active field of research for several decades and in this time most effort has been concentrated on the matching of spectral sensitivity (λ_{max}) to environmental factors, especially spectral irradiance. Such studies have identified numerous correlations between λ_{max} and the underwater light environments, although rigorous statistical methods have not been employed and many apparent correlations may be confounded by phylogenetic factors. This problem has been minimised in some studies which focused on closely related species and has been avoided by the use of modelling, principally to determine what visual pigments should best suit some defined visual task, which has often proved to have useful predictive value. The future understanding of the way in which visual pigments are adapted to the underwater environment will, however, depend on the identification visual tasks that demonstrably affect fitness: i.e. tasks that are essential for survival and reproduction. Such an experimental approach will perhaps be most successful when the visual tasks of individual species, particularly those that experience significant developmental changes, are examined in detail.

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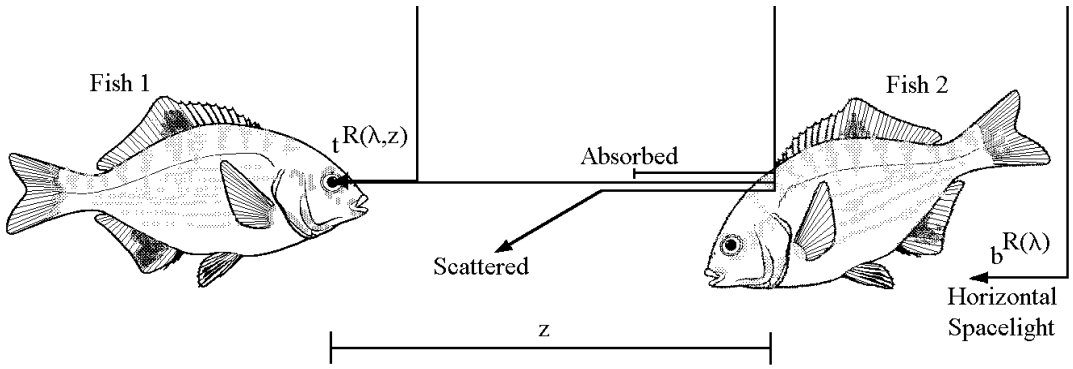

Figure Legends

Fig. 1

Light incident on fish 2, originating from all directions surrounding fish 2 but primarily from above, is reflected towards an observing fish 1 which is at a horizontal distance *z*. This radiance, R(λ*)*, which has units of photons s^{-1} nm^{-1} $steradian^{-1}$, is attenuated by absorption and scattering such that the image forming light reaching fish 1 is reduced. This image forming light is also degraded by the addition of non-image-forming "veiling" light that is scattered into the visual pathway and which reduces the contrast between radiance from target fish 2, ${}_tR(\lambda,z)$, and that of the background spacelight, ${}_bR(\lambda)$. As explained in Section 8.3, the apparent radiance, ${}_tR(\lambda,z)$, and the apparent contrast, $C(\lambda,z)$, between the target fish and the background light, are given by equations that depend on the narrow beam attenuation coefficient $\alpha(\lambda)$ and the horizontal visualization distance z.