Journal of Fish Biology (1999) **54,** 921–943
Article No. jfbi.1998.0919, available online at http://www.idealibrary.com on IDEAL

The UV visual world of fishes: a review

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(*Received 8 June 1998, Accepted 15 December 1998*)

Ultraviolet-A radiation (320–400 nm) is scattered rapidly in water. Despite this fact, UV is present in biologically useful amounts to at least 100 m deep in clear aquatic environments. Discovery of UV visual pigments with peak absorption at around 360 nm in teleost cone photoreceptors indicates that many teleost fishes may be adapted for vision in the UV range. Considering the characteristic absorption curve for visual pigments, about 18% of the downwelling light that illuminates objects at 30-m depth would be available to UV-sensitive cones. Strong scattering of UV radiation should produce unique imaging conditions as a very bright UV background in the horizontal view and a marked veiling effect that, with distance, obscures an image. Many teleosts have three, or even four, classes of cone cells mediating colour vision in their retina and one can be sensitive to UV. These UV-sensitive cones contain a visual pigment based on a unique opsin which is highly conserved between fish species. Several powerful methods exist for demonstration of UV vision, but all are rather demanding in terms of technique and equipment. Demonstration that the eye lacks UV-blocking compounds that are present in many fish eyes is a simpler method that can indicate the possibility of UV vision. The only experimental evidence for the use of UV vision by fishes is connected to planktivory: detection of UV-opaque objects at close range against a bright UV background is enhanced by the physical properties of UV light. Once present, perhaps for the function of detecting food, UV vision may well be co-opted through natural selection for other functions. Recent discovery that UV vision is critically important for mate choice in some birds and lizards is a strong object lesson for fish ecologists and behaviourists. Other possible functions amount to far more than merely adding a fourth dimension to the visible spectrum. Since UV is scattered so effectively in water, it may be useful for social signalling at short range and reduce the possibility of detection by other, illegitimate, receivers. Since humans are blind to UV light, we may be significantly in error, in many cases, in our attempts to understand and evaluate visual aspects of fish behaviour. A survey of the reflectance properties of skin pigments in fishes reveals a rich array of pigments with reflectance peaks in the UV. For example, the same yellow to our eyes may comprise two perceptually different colours to fish, yellow and UV-yellow. It is clearly necessary for us to anticipate that many fishes may have some form of UV vision.

Key words: ultraviolet; vision; coloration; behaviour; evolution; opsin.

INTRODUCTION

Zoologists recognize routinely that the Umwelt or perceptual world of their animal subjects may escape our own sensory abilities. Olfaction, ultrasound and

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electro-reception are recognized as sensory dimensions of a form that we can appreciate only in the most general terms. Ethologists and behavioural ecologists are particularly troubled by the limitations that our sensory systems pose to our research abilities. However, most of us have assumed that even though differences exist clearly in visual capabilities between us and our subjects, we are not missing any major components of their coloration. We recognize that possibly each observer will perceive the spectral reflections from an object as a slightly different colour. An animal's perception that two reflection patterns differ might be based on differences between their hue, brightness or degree of saturation. We might have a different perception of these parameters, but should agree with the animal that the reflection patterns are different. A recent surge in the discovery of the possible importance of UV light in the lives of fishes has, however, cast doubt on this homocentric assumption. Just as the invertebrate biologists, and more recently the avian biologists, have learned, we may be blind to many interesting and critical aspects of the coloration of fishes and their perception of the environment. It is problematic to even consider that colour can be defined as a property of an object rather than the complex interaction between the object, the available light, the environment and the sensory properties of the observer. For the sake of simplicity, we will refer to the colour of objects always with the precaution that this colour is a perception of the spectral reflection (and emission) properties of the object that must depend on many other factors including the sensory capabilities of the observer. This review focuses attention on the current state of our knowledge regarding UV vision and coloration in fishes.

UV LIGHT IN THE SEA—WHAT'S OUT THERE?

Wavelengths shorter than 400 nm are referred to as ultraviolet (UV), but due to ozone absorption in the upper atmosphere, little natural UV light is available to organisms at wavelengths much shorter than about 300 nm. In the 1950s, it was established that UV-A radiation (320–400 nm) penetrates to reasonable depths in clear seas. Because it is attenuated about as rapidly as longer wavelengths in the visible range (>550 nm; Smith & Baker, 1979; McFarland, 1986; Loew & McFarland, 1990) it was considered of little significance in the visual behaviour of aquatic organisms. Several factors have led to a renewed interest in submarine UV light. Most notable is the discovery of the ozone hole and the demonstration that UV light may have a deleterious effect on algae (Larned, 1995) and many invertebrates (corals; Jokiel, 1980). For fish biologists, the discovery that UV visual cone pigments are present in many fishes (Merker, 1939; Avery *et al.*, 1983; Hawryshyn & Beauchamp, 1985; Bowmaker, 1991; Palacios *et al.*, 1996, 1998; reviewed in Douglas *et al.*, 1989) was a seminal event. The development of modern computer-operated spectroradiometers has now provided the technical ability to establish, in detail, the spectral distribution of light underwater, including UV (Tyler & Smith, 1970; Baker & Smith, 1982; Dunne & Brown, 1996; Loew *et al.*, 1996; Novales Flamarique & Hawryshyn, 1997).

Here we emphasize that UV-A light constitutes a high proportion of the total number of photons available for vision underwater, especially in clear tropical

seas [Fig. 1(a)]. For example, near the surface, the number of UV-A photons approaches 40% of the total for the horizontal and downward directed lines of sight. When looking up, although the absolute UV intensity is higher, the percentage of UV-A declines: more long-wavelength photons are present as the angle of sight approaches that of the solar axis. Cones containing a visual pigment with an absorption maximum near 360 nm [Fig. 1(a)] absorb UV-A radiation effectively along all lines of sight. Combining such a cone type with another more sensitive to the blue region of the spectrum, as demonstrated in several pomacentrids (McFarland & Loew, 1994), would maximize photoabsorption of horizontal and upwelling light and provide a high degree of sensitivity to the background space light.

Because of the molecular properties of water and any suspended particles, as the wavelength of the light penerating the sea decreases, the scattering of photons increases. The optical path over which UV light is transmitted, as compared to the blue region of the spectrum, is shortened, and simultaneously the veiling brightness increases (Lythgoe, 1979). Therefore, vision in the near-UV is most likely effective over only short distances, e.g. <5 m. During the day the amount of UV light near the surface is well above the usual photopic visual threshold of many fishes (approximately 10^{14}–10^{15} photons m^{-2} s^{-1}, calculated from Blaxter, 1988). Even in coastal waters and many freshwater habitats, where particulates and dissolved organics will attenuate UV-A light further, the number of UV photons at moderate depths remains well above the visual thresholds of most fishes.

It has been established for a long time that in clear seas the wavelengths that are transmitted maximally into the depths of the euphotic zone are centred in the blue region of the spectrum (*c.* 450–470 nm, Jerlov, 1968). Given that UV light is attenuated more rapidly, one can ask how deep it can penetrate and still retain sufficient intensity to stimulate cone vision. Deep-sea fish appear to lack UV-sensitive visual pigments (Douglas & Partridge, 1997), but the answer for other fishes remains to be established. Some species of deep-sea crustaceans that inhabit depths from 400 to 600 m are, however, sensitive to very dim UV-A light (flux rates of *c.* 10^{11}–10^{12} photons m^{-2} s^{-1}, Frank & Widder, 1996). An UV-sensitive photomultiplier-based radiometer revealed that flux rates of 10^{10} photons m^{-2} s^{-1} existed at 450 m depth. If we assume conservatively that the threshold for cone vision in a surface-dwelling fish is near 10^{14} photons m^{-2} s^{-1} (Blaxter, 1988), then there should be enough UV photons during the day in a clear sea to sustain visual sensitivity to a depth of 200 m. With increased depth, however, the blue region of the spectrum dominates increasingly [Fig. 1(b)]. At 30 m, *c.* 18% of the available downwelling light is between 300 and 420 nm. This declines to 14% at 90 m, and 5% at 150 m. Clearly there is sufficient UV-A light in clear seas to sustain vision to depths exceeding 100 m, but the significance of UV vision in fishes inhabiting these depths remains to be determined.

UV VISION—HOW IS UV RADIATION RECEIVED?

The rods and cones of vertebrates are sensitive to light because they possess visual pigments, photosensitive molecules consisting of a protein (opsin) combined with a small (20-carbon), fat-soluble molecule related to vitamin A.

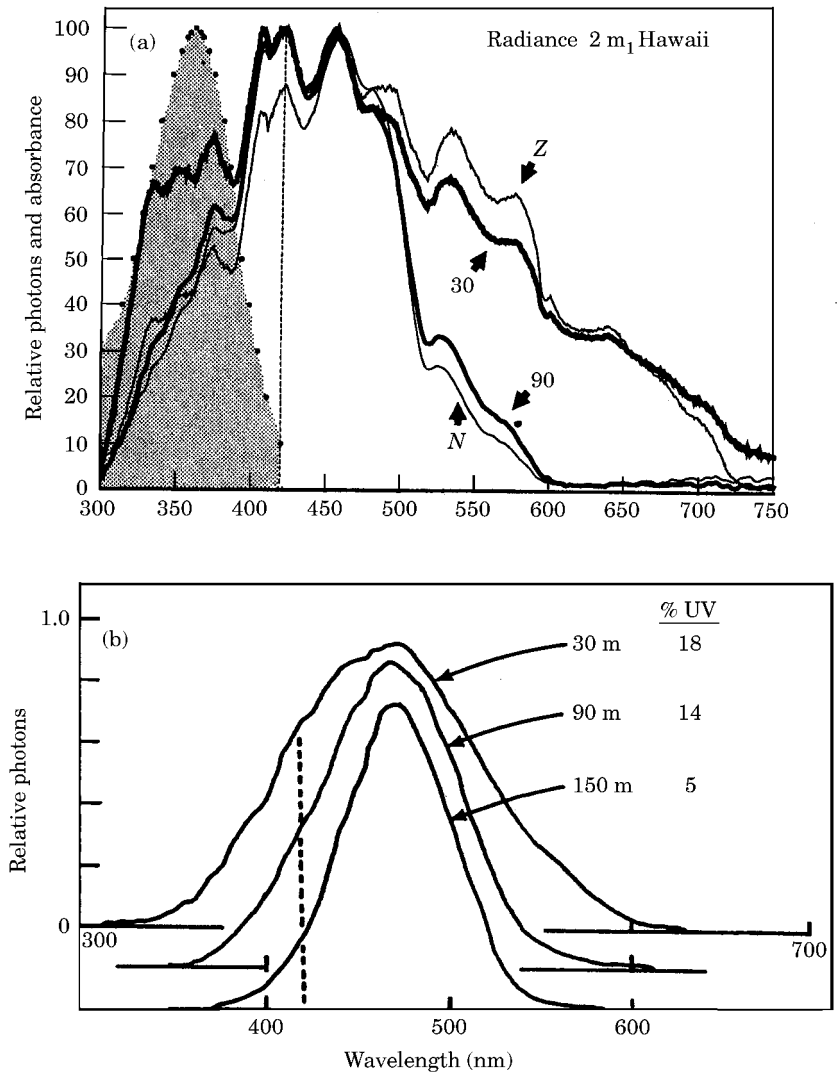

FIG. 1. Spectral distribution for submarine light in clear seas. (a) Relative photon radiance at 2 m beneath the water surface along four lines of sight 1 mile offshore from Kaneohe Bay, Oahu, Hawaii (Loew & McFarland, unpubl. data). The arrows point to each line of sight *Z* is the zenith measured radiance directly overhead, '30' is the radiance 30° from the zenith, '90' is horizontal radiance and *N* is upwelling radiance from the nadir. The spectra were recorded with a Model P51000 Ocean Optics spectrometer calibrated to read in the number of photons $m^{-2} s^{-1} nm^{-1} sr^{-1}$. The dark circles surrounding the stippled area represent the relative absorbance of a retinal$_1$ based visual pigment; the dotted curve is a template generated for a visual pigment with a maximum absorbance located at 360 nm in the UV (see Partridge & DeGrip, 1991, for details about the template). The dashed vertical line at 420 nm represents the long-tail wavelength at which this visual pigment would absorb 10% of the available photons. Solid lines are spectra collected around 1820 hours. The dotted line indicates 420 nm. The relative number of photons between 300 and 420 nm compared to the total photons between 300 and 750 nm for each spectral curve are: Z=24%, 30=32%, 90=38% and N=38%. Note that a visual pigment with maximum absorbance centred at 360 nm would absorb mostly in the UV-A and only slightly in the deep blue or indigo region of the underwater spectra. (b) Relative photon irradiance at increasing depths off of Cape Hatteras. Percentages are the relative amount of UV photons between 300 and 420 nm compared to the total photons at each depth. Spectra have been offset and redrawn from Fig. 3 in Frank & Widder (1996).

Characteristically, fish have rods containing one opsin and several spectral classes of cones, each with a different opsin. Rods function in dim light, and cones, which subserve colour vision, require more light. Rods are maximally sensitive at about 500 ± 20 nm. Cones are more diverse and can have λ_{max} in a broader spectral region that extends from about 360 nm in the UV to 620 nm in the red, depending primarily on the opsin. The C_{20} chromophore, however, also influences the λ_{max} because there are two forms: retinal$_1$, the aldehyde of vitamin A, and 3,4-dehydroretinal (retinal$_2$), which differs by the presence of an additional double bond (Bridges, 1972). Visual pigments that have the same opsin but have retinal$_2$ instead of retinal$_1$ as their chromophore absorb at longer wavelengths. The difference which is small in the violet region of the spectrum, is about 20 nm for rods or mid-wavelength cones, and increases to more than 60 nm for long-wavelength cones (Tsin & Beatty, 1978; Whitmore & Bowmaker, 1989). Some fish have retinal$_1$, others retinal$_2$, and still others a mixture that can vary with conditions of light, temperature, or stage of the life cycle (Beatty, 1984). Characteristically, a photoreceptor cell expresses the gene for a single opsin, but at times it may contain both retinal$_1$ and retinal$_2$, thus two visual pigments.

The principal absorption band of visual pigments is broad (*c.* 100 nm half-band width). All of the pigments with λ_{max} in the visible region of the spectrum have a shoulder of absorption at shorter wavelengths which extends through the near UV, and all have a secondary absorption band at about 280 nm, which is due to aromatic amino acids in the opsin. There is virtually no natural light at the surface of the earth at wavelengths shorter than 300 nm, so the protein band does not participate in visual excitation. As all visual pigments absorb light at 300–400 nm, however, they can be excited in this spectral region. Many animals, however, have UV-absorbing lenses that prevent light at 300–400 nm from reaching the retina (Thorpe *et al.*, 1993).

In what follows, UV vision refers to the presence of cones containing a UV visual pigment with λ_{max} characteristically at 360–380 nm. The presence of UV cones may increase the absolute sensitivity of the retina to UV light, but more importantly, it provides an opportunity for UV to make a unique contribution to the perception of colour. Such UV visual pigments are present in many species of fish. Indeed, they are found in all classes of vertebrates, although in mammals they are known in only a few rodents (Jacobs, 1992).

The presence of the UV-sensitive pigments can vary ontogenetically. Juvenile salmonids, yellow perch *Perca flavescens* (Mitchill) and bluegill sunfish *Lepomis macrochirus* Rafinesque possess UV cones when in the planktivorous foraging mode, but lose them when they switch to other feeding modes (review in Bowmaker, 1990). In contrast, goldfish *Carassius auratus* L., many minnows and several damselfishes possess UV photoreceptors in the adult stages. Others, such as skates (Rajidae), have an all-rod retina and are thus unlikely candidates for UV vision. Many fish possess UV-blocking compounds in the cornea and lens (Kennedy & Milkman, 1956; Douglas & McGuigan, 1989; Dunlap *et al.*, 1989; Thorpe *et al.*, 1993) that render them incapable of effective UV vision. M. Posner (pers. comm.) has found that, in flatfish, the lens concentrates the UV-blocking compounds found in the humour of the eye, but that control of the variable level of these compounds is accomplished elsewhere. However,

for the vast majority of fishes, there is little or no information concerning their potential for vision in the UV.

A molecular analysis of the genes encoding the UV opsins reveals that the corresponding proteins may be highly conserved in teleosts. The zebrafish *Brachydanio rerio* (Hamilton) UV opsin gene was cloned and sequenced recently (Vihtelic *et al*., 1998). The putative zebrafish UV opsin possessed 86% amino acid identity with the goldfish UV opsin (Hisatomi *et al*., 1996), but only 41·9, 43·9 and 44·0% amino acid identity with the goldfish rod, blue, and red opsins, respectively (Johnson *et al*., 1993). Similarly, the two different goldfish green opsin proteins possess *c.* 40% amino acid identity with this putative zebrafish UV opsin. Further comparison revealed that this zebrafish UV opsin possesses only 40–50% amino acid identity with the recently isolated zebrafish rod, blue, red, and two different green opsins (Vihtelic *et al*., 1999).

UV VISION—HOW CAN WE DEMONSTRATE IT?

Demonstration of UV vision can use several methods, each with its own advantages and drawbacks. The simplest and least direct is to measure the absorption of the ocular media, particularly the lens. Presence of UV absorption between 300 and 400 nm makes it unlikely that the retina has UV cones (Thorpe *et al*., 1993). It has yet to be established whether it is a reliable indicator of UV vision to demonstrate that UV radiation is allowed to reach the retina without significant absorption.

The cones that contain the UV visual pigments are small, and it is difficult to study cone pigments in solution by chemical methods of protein extraction. There are several optical and physiological techniques, however, for identifying the presence of UV cones and determining the wavelengths to which each class is sensitive.

Microspectrophotometry (MSP), as the name implies, is spectrophotometry performed on very small objects, using microscope optics. Ordinarily, this is done by passing a beam of light laterally through the outer segment of a single rod or cone. Since the visual pigments are bleached quickly when exposed to light, the intensity of the measuring beam must be kept as low as possible. Because the cells are small, care must be taken so that the beam is contained entirely within the cell. Little light reaches the instrument's detector and the signal is overlain by shot noise due to statistical variation in the flux of photons (Fig. 2; Loew & Wahl, 1991).

Alternatively, it is possible to measure the spectral sensitivity of individual cells by biophysical techniques. Trans-membrane voltages (in the range of mV) can be recorded with intracellular microelectrodes. Or one can draw the outer segment of an intact cone cell snugly into a small pipette electrode and measure the photocurrents (in the range of nA) that occur when the cell is excited by light. As with MSP, this technique requires a highly controlled light source and a way of varying the wavelength. In addition, it requires a means of measuring and controlling the light energy and the duration of exposure at each wavelength. Spectral sensitivity is measured by determining the photon flux required to produce some criterion amount of excitation at each wavelength (Fig. 3; Palacios *et al*., 1996, 1998).

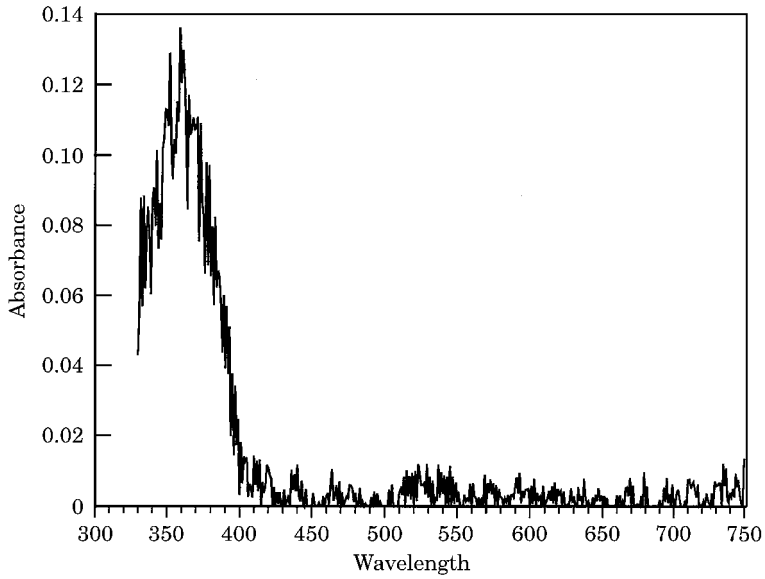

FIG. 2. Normalized spectral absorbance of a short wavelength sensitive cone from an adult Eastern Golden Shiner *Notemigonus crysoleucas* (Mitchill) recorded by microspectrophotometry. Maximum sensitivity is *c.* 355 nm. The vertical scale is relative absorbance (optical density) which is a measure of light absorption. With permission (Loew & McFarland, unpubl. data).

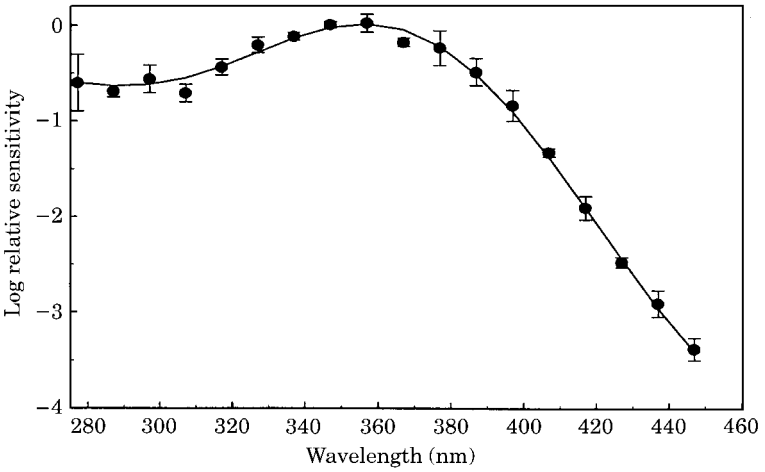

FIG. 3. Spectral sensitivity of the UV cones of *Danio aequipinnatus* measured on single cells with suction pipette electrodes. Maximum sensitivity is at 358 nm. Each point is an average of three to 11 cones, and the error bars indicate ± 1 S.D. Note that unlike measurements of light absorption (as in Fig. 2), physiological measurements of sensitivity can extend over several log units, thus to long wavelengths inaccessible by microspectrophotometry. This fish has three other spectral classes of cone, with peak sensitivities at 560, 480, 408 nm. (From Palacios *et al.*, 1996.)

A somewhat easier procedure, although one giving less precise information, is to record the electroretinogram (ERG). This can be accomplished on living fish with relatively large, external electrodes. The ERG, however, reflects the summed activity of neurones and glial cells in the retina, and its interpretation is

therefore more problematic than measurements made on individual cells. In principle, however, it is possible to provide evidence for the presence of UV receptors by measuring spectral sensitivity in the presence of a yellow adapting light that desensitizes all of the other cones (Chen *et al.*, 1984; Chen & Goldsmith, 1986; Hawryshyn & McFarland, 1987; Hawryshyn, 1992; van Roessel *et al.*, 1997).

Cardiac modulations, conditioned through vagal inhibition of heart rate, have been utilized to provide a more general physiological response to UV stimuli. This technique has revealed that goldfish and juvenile rainbow trout *Oncorhynchus mykiss* (Walbaum) are sensitive to UV light and, also, that they respond to the E-vector orientation of polarized UV light (Hawryshyn & McFarland, 1987; Hawryshyn, 1992). The method utilizes a multichannel optical system for control of signal light intensity and wavelength, and exposes the fish's eye to a yellow adapting light to isolate the UV response by bleaching the other cone cells. The apparatus has been adapted for electrophysiological measurement of optic nerve and tectal responses.

Cloning the zebrafish UV opsin provides a molecular method for examining UV visual receptors which is based on the significant amino acid homology between the UV opsins of other teleost fishes. A polyclonal antiserum was created against an *Escherichia coli* fusion protein that contained the first 58 amino acids from the zebrafish UV opsin, and was used to examine the spatial distribution of the UV opsin in the zebrafish retina. Indirect immunofluorescence revealed that the UV opsin's expression was restricted to the area containing the outer segments of the short single cones [Fig. 4(a) and (b)]. These cones were hypothesized to be the UV light-sensitive photoreceptor cells (Raymond *et al.*, 1993, 1996; Robinson *et al.*, 1993; Hisatomi *et al.*, 1996). Thus the cell-specific UV opsin expression patterns can be determined and correlated with the spectral sensitivities of the UV cones, as has been done with both zebrafish (Fig. 3) and goldfish (Palacios *et al.*, 1996, 1998).

Photoreceptor cells that have been made metabolically active can be identified histochemically with the redox probe nitroblue tetrazolium chloride, which is reduced to an insoluble blue compound by active mitochondria. This technique has been used recently to distinguish UV from violet-sensitive cones in the starling *Sturnus vulgaris* retina by irradiating opened eyecups with either 381-nm or 434-nm light to activate either the UV or the violet-sensitive cones, respectively (Hart *et al.*, 1998).

Behavioural experiments can also be used to reveal UV sensitivity, and they are essential for demonstrating colour vision. In an elegant example of the latter, Neumeyer (1992) has reported an extensive series of experiments on the goldfish that address both the presence of colour vision and the role of UV cones. The fish were taught to distinguish a monochromatic training light from a test field containing a variable mixture of two other wavelengths, using food as reward. Fish could not distinguish a 404-nm training field from a test field containing a mixture of 45% 434 nm and 55% 367 nm. Such metameric colour matches are an important source of data on which theories of colour vision are based. This particular colour match provides direct evidence for the participation of the UV receptor in the colour vision of goldfish. On the basis of other experiments, Neumeyer (1992) has concluded further that the colour vision of the goldfish is

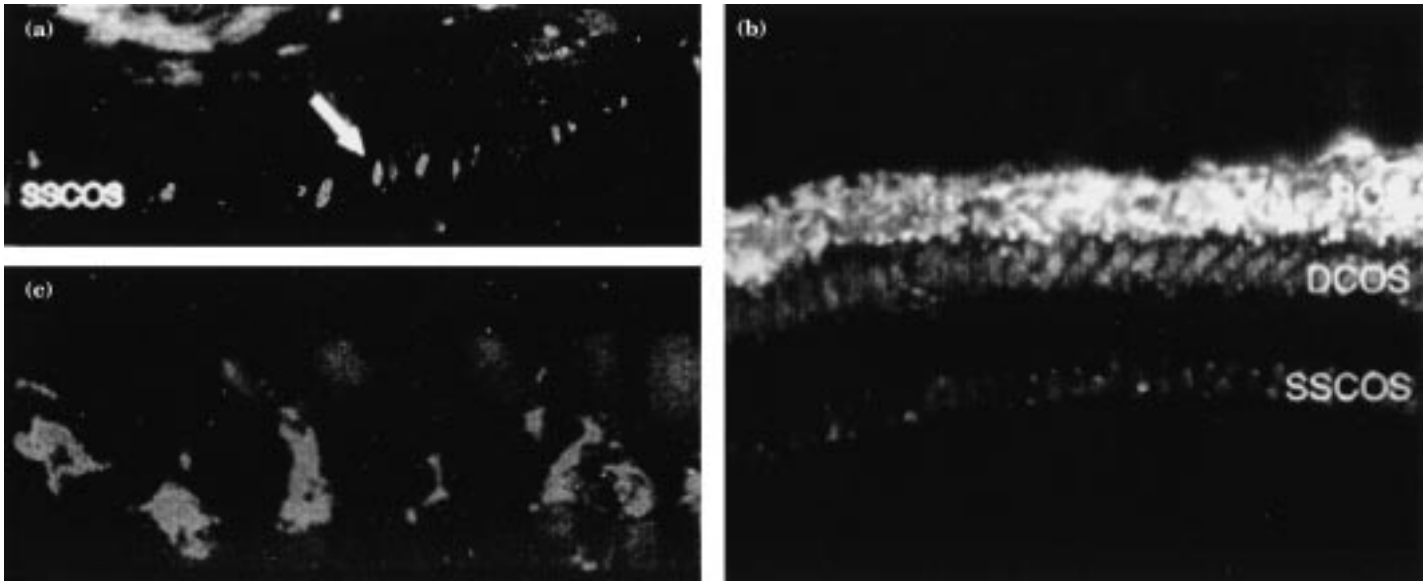

FIG. 4. Immunolocalization of the zebrafish UV opsin to the short single cone outer segments. Immunopurified polyclonal antisera generated against either the amino terminus of the UV opsin (a) and (b) or the rod opsin (c) were incubated with frozen retinal tissue sections and detected with a Cy3-conjugated goat anti-rabbit secondary antibody. The Cy3 signal in the UV opsin incubated tissue is restricted to the short single cone outer segments (SSCOS), while a different antibody generated against a zebrafish retinal protein stains the rod outer segments (ROS), the double cone outer segments (DCOS), and the short single cone outer segments (SSCOS).

tetrachromatic. The goldfish indeed has four cones, with λ_{max} at about 356, 452, 533, and 623 nm (reviewed in Palacios *et al.*, 1998).

In principle, other sorts of behavioural experiments can provide information on the presence of UV sensitivity, but without necessarily showing the involvement of UV cones in colour vision. For example, in the rudd *Scardinius erythrophthalmus* (L.) the action spectrum for a two-choice discrimination with food reward at the monochromatic window peaked in the deep violet (UV was not studied in this experiment), with secondary maxima at *c.* 500 and 600 nm. At least three cones were therefore participating in this behaviour, but the influence of the short-wavelength cones was greatest. By contrast, the startle response to sudden movement in the visual field appeared to be driven exclusively by the long-wavelength cones (Muntz, 1975).

Fish behaviour may include both colour vision and wavelength-dependent behaviour in which specific cues (e.g. releasers) are filtered and interpreted in stereotyped ways that are relatively inflexible and not susceptible to change by learning. The latter concept comes primarily from the study of insect behaviour, but it may have relevance for some vertebrates (Goldsmith, 1994).

UV COLORATION—WHAT'S OUT THERE?

Lacking UV sensitivity, the human visual system cannot interpret colours and colour patterns based on their UV content. Determining the presence of UV in any animal's colour display and quantifying it relative to other spectral regions is an important first step. Two approaches have been taken, UV videography and measurements of spectral reflection (for studies of birds see Silberglied, 1979; Burkhardt, 1983; Bennett *et al.*, 1994, 1997). It is also important to ascertain whether any UV reflectance is biologically significant. Experimental studies are demanded, but initial descriptive work can yield important clues as to biological function.

The spectral reflection of body colours in a total of 159 species in 26 families of reef fishes has been quantified using Sub-Spec, an underwater spectroradiometer (Marshall, 1996; Table I). One hundred of these species (*c.* 60%) exhibit one or more colours that include UV wavelengths, suggesting the possible participation of UV signals in the colour world of the reef. Very few examples exist of a pure UV colour. More often we perceive the pigment as having a colour, but it also contains a significant invisible UV component (Fig. 5). Also, no examples are yet known where an UV pattern emerges (when viewed with the UV-sensitive camera system), from a background that is a uniform colour in the 400–700-nm human visible range. Such secret signals are known only in flowers (Silberglied, 1979) and, possibly, anoles (Fleishman *et al.*, 1993). This in no way detracts from the possible significance of UV to fish, as the relative contrasts of colour patterns containing UV elements will be very different to a visual system with UV sensitivity compared to one without (Fig. 6). The possible uses of UV colours are examined further after an examination of the colours themselves and their anatomical position.

For fish with four visual pigments, the familiar three-colour visual system or colour space based on human perception is very likely inappropriate. In such cases, a four-dimensional system such as that suggested for birds (Goldsmith,

TABLE I. Families of reef fish in which colour reflectance has been measured in some species and the number of species showing a large reflection of UV radiation

Family	Species with UV	Species examined
Syngnathidae	0	1
Priacanthidae	0	1
Caesionidae	2	2
Pseudochromidae	3	3
Chaetodontidae	15	21
Pomacanthidae	9	14
Pomacentridae	10	17
Serranidae	6	9
Grammatidae	1	1
Aulostomidae	0	1
Gobiidae	3	4
Acanthuridae	11	14
Balistidae	1	5
Labridae	17	27
Scaridae	6	16
Haemulidae	1	3
Lethrinidae	2	2
Mullidae	1	3
Holocentridae	1	1
Zanclidae	1	1
Siganidae	0	2
Blenniidae	2	2
Scombridae	2	2
Monacanthidae	2	3
Tetraodontidae	2	2
Ostraciidae	2	2
Total	100	159

1990, 1994) and goldfish (Neumeyer, 1992) is more appropriate. The apparently limitless colours of reef fish can be categorized into those that do [Fig. 5(a)] and do not [Fig. 5(b)] have a large reflection of UV radiation either as a separate peak below 400 nm (e.g. yellow/UV and green/UV) or as part of a colour which spans the intersection between the human visible and the UV (e.g. white/UV or blue/UV). It is notable that all categories of fish colours described by humans as, for example, blue, green, yellow, orange or red exist both with and without a UV component, an indistinguishable difference to us and suggestive of a function where UV vision is present.

In common with all animals whose colour is epidermal in origin, fish colours originate in specialized cells named iridophores or chromatophores (Fox & Vevers, 1960). Chromatophores contain pigments such as carotenoids or flavins, which determine the colour of the cell. Many yellows, oranges and reds for instance are produced by carotenoid pigments (Fox, 1953). Shorter-wavelength colours such as UV, blue and also the silvery appearance of fish are more commonly the result of structural coloration produced by iridophores (Denton & Nicol, 1966; Land, 1972). Colours can also result from a combination of

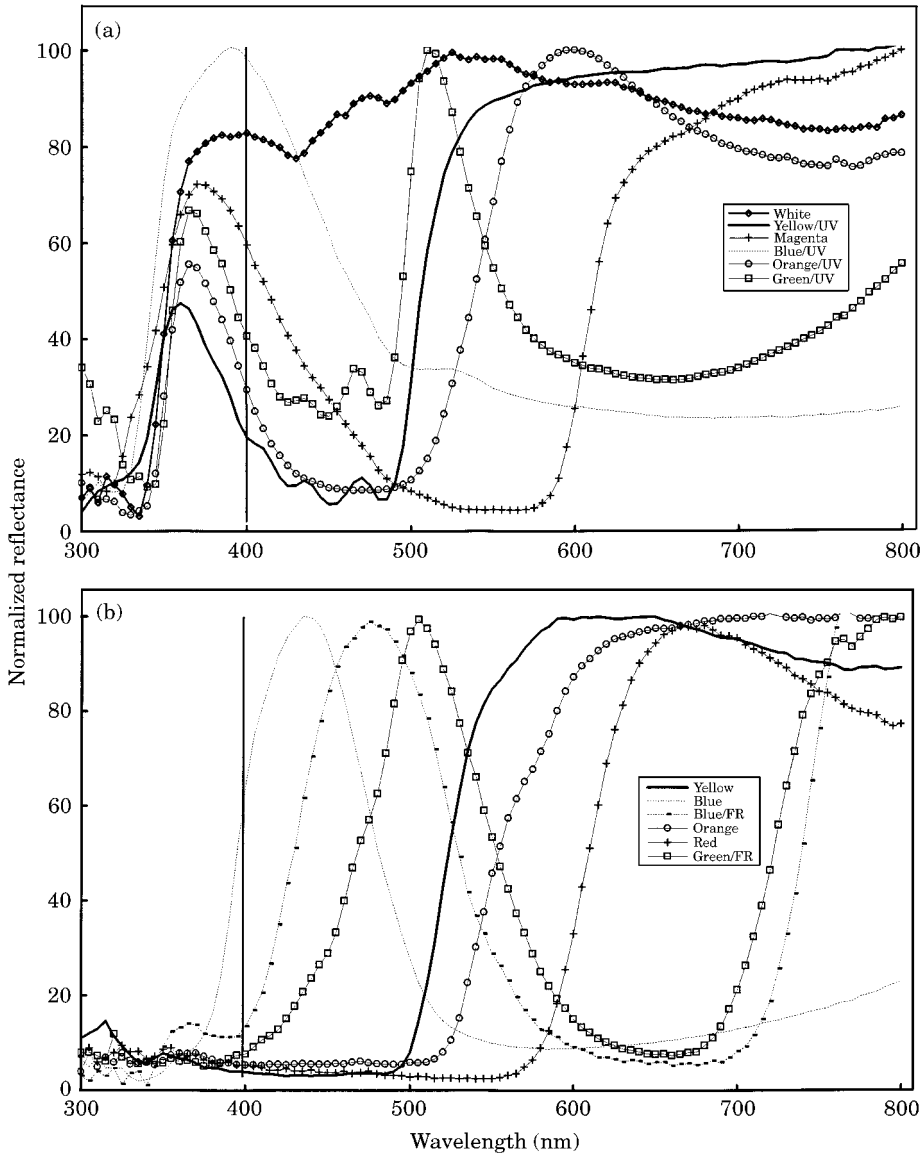

FIG. 5. Examples of reflectance spectra in fish colours (a) containing and (b) not containing UV. The human visual system is sensitive to wavelengths to the right of the vertical bar at 400 nm. To the left of this bar the UV wavelengths between 300 and 400 nm may be visible to fish. Of the 27 categories of fish colours recognizable (Marshall, unpubl. obs.), 14 possess a UV component. The six examples shown in (a) are plotted as normalized reflectance spectra for ease of comparison. They are taken from the following fish and body areas: white/UV, *Sparasoma viride* (Bonnaterre) (juv.) spot on flank; yellow/UV, *Acanthurus japonicus* (Schmidt) dorsal fin; magenta, *Pseudochromis paccagnellae* (Axelrod) head; blue/UV, *Valenciennea strigata* (Broussonet) opercular stripe; orange/UV, *Halichoeres hortulanus* (Lacépède) head stripe; green/UV, *Thalassoma bifasciatum* (Bloch) tail.

structural and pigmentary colours (e.g. green is often produced by a combination of structural blue and pigmentary yellow, Fox & Vevers, 1960). Double-peaked colours such as those in Fig. 5 are also likely to be combinatorial, with the UV

reflectance resulting from structural coloration. However, so little work has been done in this area (Kasukawa *et al.*, 1987) that such conclusions are highly speculative. Changes in visible coloration of fishes are well known (Townsend, 1929), but changes in the UV component of colours have yet to be considered.

UV colours are found on all body regions, but often occur in three patterns: (a) on the fins, often as a rim around the edge or in a position which is less obvious with the fins folded (e.g. the dorsal fin edge in *Chaetodon auriga* (Forsskål) or all fin edges of *Centropyge bispinosus* (Günther), (b) on the head, usually in the form of an anteriorly detected pattern of facial stripes (e.g. the Caribbean hamlets and many labrids), (c) on the flanks as spots, commas or stripes [all of which may spread to the fins, e.g. *Plectropomus leopardus* (Lacépède) or *Pygoplites diacanthus* (Boddaert)]. In a few species (such as those in Fig. 6), relatively large body regions or blocks contain UV reflectance. Fin and facial markings are thought to be biologically significant, as these are often shown in lateral or frontal dynamic displays (Eibl-Eibesfeldt, 1970).

UV VISION—FUNCTION AND ADAPTIVE SIGNIFICANCE

Allowing UV radiation to strike the retina probably imposes a metabolic cost on the individual that must be offset by benefits of UV vision. UV radiation, even the longer-wavelength UV-A, damages the retina (Collier & Zigman, 1987; Zigman, 1993; Zigman *et al.*, 1996) and will increase the degree of chromatic aberration (Muntz, 1973). Trout that lose UV vision with age show a parallel increase in absorption of UV by their lens thus protecting the retina (Douglas, 1989). This suggests strongly that we may find some critical functions that are served best by vision in the UV range.

As discussed above, although near-UV wavelengths penetrate clear sea water well [Fig. 1(a) and (b)], the ability of animals to see detail in the UV at any distance is severely limited. The effects of scattering are particularly obvious when comparing images acquired simultaneously at medium and short wavelengths. Scattering can make nearby objects stand out in silhouette and more distant ones nearly disappear behind a veil.

Special significance has been attributed to the UV component of sexual display in reptiles (Fleishman *et al.*, 1993), birds (Bennett *et al.*, 1994, 1997; Andersson & Amundsen, 1997) and insects (Arikawa *et al.*, 1987). Several potential functions for UV vision in marine waters are given below, listed in approximate order of the amount of current evidence supporting each.

IMAGING MIDWATER OBJECTS AGAINST THE BRIGHT UV UNDERWATER SPACE LIGHT

Many small, planktivorous fishes feed effectively under UV illumination alone (Loew *et al.*, 1993, 1996; Browman *et al.*, 1994), and among marine fishes, planktivorous pomacentrids are known to be UV photosensitive (McFarland & Loew, 1994). UV vision could be effective at larger ranges for detecting prey, predators and competitors (Figs 7 and 8) (see also Cronin *et al.*, 1994).

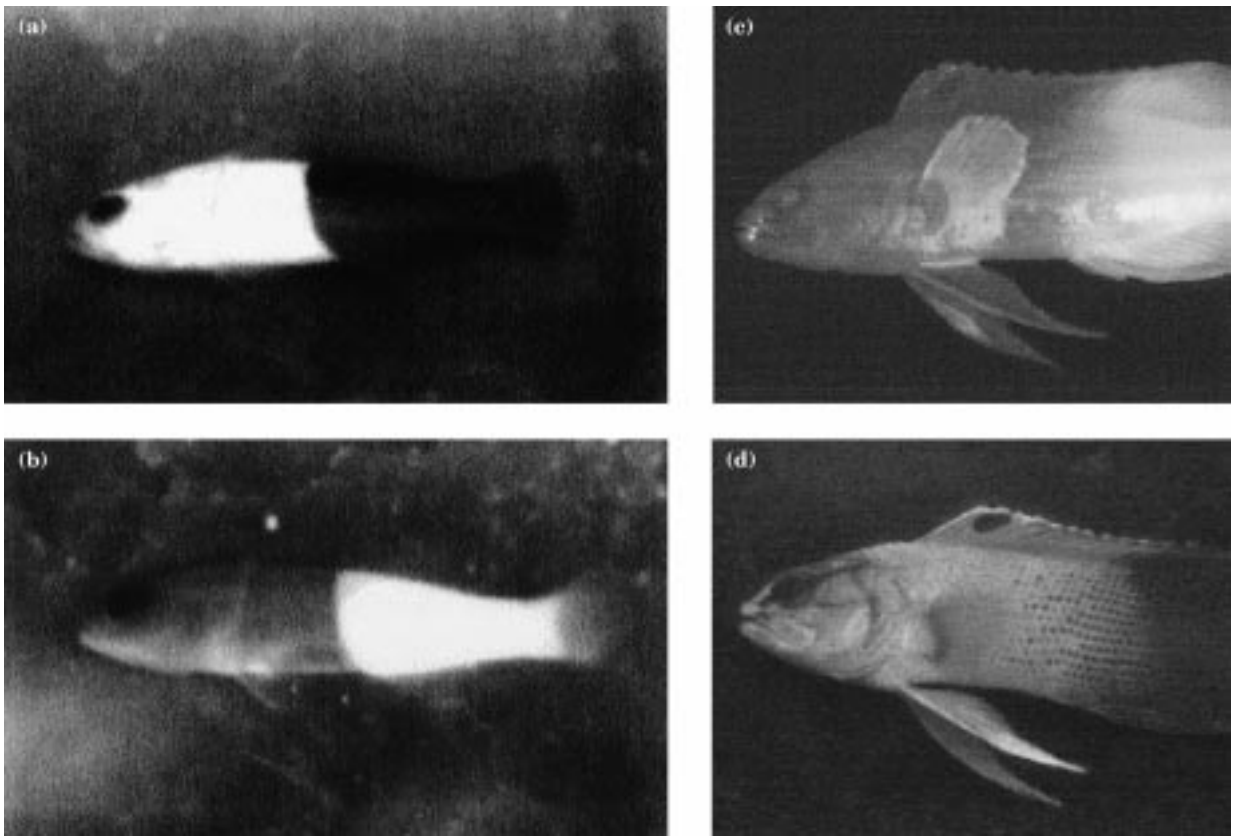

FIG. 6. (a)–(d).

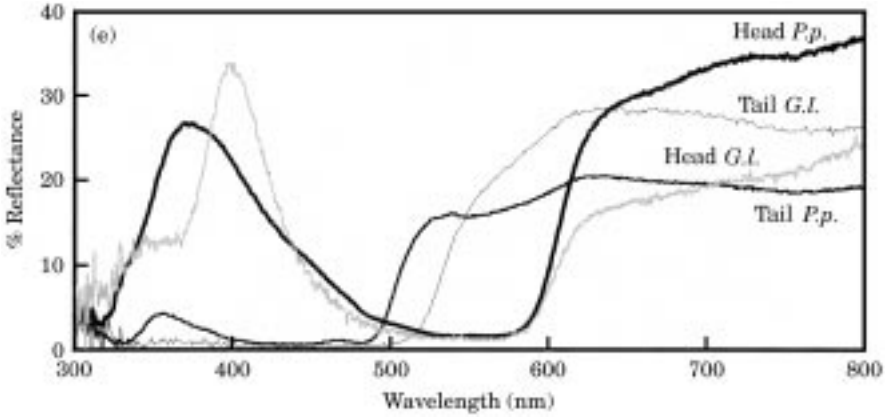

FIG. 6 (e)

FIG. 6. Video images of fish taken with a camera the sensitivity of which could be switched between an approximation of human visible (400–700 nm) and UV wavelengths (350–400 nm). Such images indicate the possible advantages of extending visual sensitivity into the UV. (a) and (b) *Pseudochromis paccagnellae* which to the human visual system has a bright yellow tail and a dark magenta head. The fish was video-taped at 15 m on the Great Barrier Reef where UV illumination is still abundant. Note the bright appearance of the magenta head in (a) due to the peak in UV reflectance at 375 nm and the dark appearance of the tail in this waveband as this yellow has little UV reflectance; see (e) and compare to the yellow/UV in (b). In the human visible waveband from 400 to 700 nm this contrast pattern is reversed. (c) and (d) *Gramma loreto* a Caribbean reef fish showing remarkable convergence in colour pattern with *P. paccagnellae*. The head is magenta and the tail yellow, the transition between the two colours being more graded than in *P. paccagnellae.* Note the enhanced detail in the UV image. (e) The reflectance spectra of *P. paccagnellae* and *G. loreto*.

NAVIGATION AND ORIENTATION USING UV POLARIZATION PATTERNS

This has never been conclusively demonstrated, but it is likely to occur in salmonids and possibly other fishes (Hawryshyn & McFarland, 1987; Hawryshyn & Bolger, 1991; Hawryshyn, 1992; Parkyn & Hawryshyn, 1993).

RECOGNITION OF SPECIES-SPECIFIC UV COLOUR PATTERNS

Again, this has not been demonstrated, but in view of the striking patterns described above, it probably occurs in some species.

AVOIDANCE OF EXCESSIVE UV PHOTOEXPOSURE

UV photosensitivity exists in several species of juveniles or small fishes which are likely to find themselves occasionally near the surface where UV photoexposure may be extreme (Harosi & Hashimoto, 1983; Bowmaker *et al.*, 1991; Hawryshyn & Harosi, 1991; Browman & Hawryshyn, 1994; Kunz *et al.*, 1994; McFarland & Loew, 1994; Palacios *et al.*, 1996), and such sensitivity may provide them with an awareness of elevated UV irradiance levels.

ANALYSIS AND IMAGING OF POLARIZED UV REFLECTANCE PATTERNS

This and the following two potential uses of UV vision have not been investigated, but may well apply to at least some fish species.

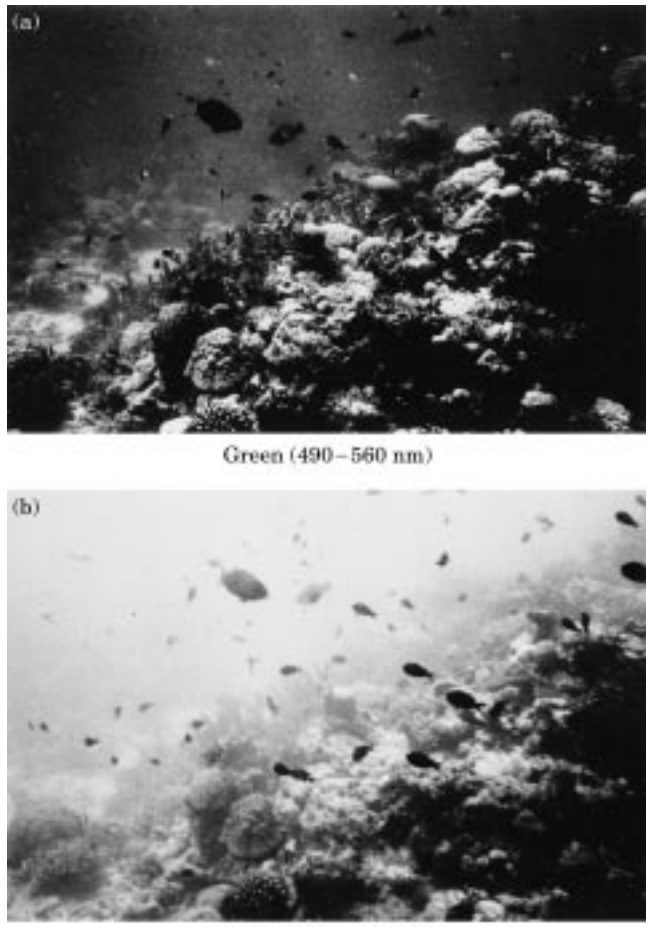

FIG. 7. Underwater images taken simultaneously in the green [(a), Corning 4-64 filter] and in the ultraviolet [(b), Corning 7-60 filter]. These images were acquired on panchromatic film (Kodak Tri-X; push-processed to 1600 ASA) using the indicated filter with Nikonos 50-mm lenses, at a shallow depth (<10 m) near midday on MacGillivray's Reef, near Lizard Island, Australia. Note the bright background light apparent in the ultraviolet, which silhouettes fish strongly, even against the reef only a few metres distant from the camera. Spectral ranges refer to wavelengths estimated to contribute to the photographic image, taking filter and lens transmission spectra into account.

SIGNALLING IN THE UV

Such signals might be either of two types.

(1) Broadcast signals such as the bright colour patterns of many coral reef species should have broad areas of contrasting UV absorption and reflectance. This could be accomplished by having a constant UV reflection in the body and choosing the appropriate background for contrast, or by having contrasting zones within the body. Since broadcast signals are often intended for a broad range of signal receivers, UV contrast should be accompanied by contrast in the longer wavelengths as well. If so, a lack of UV detection equipment does not mean that the observer will always miss

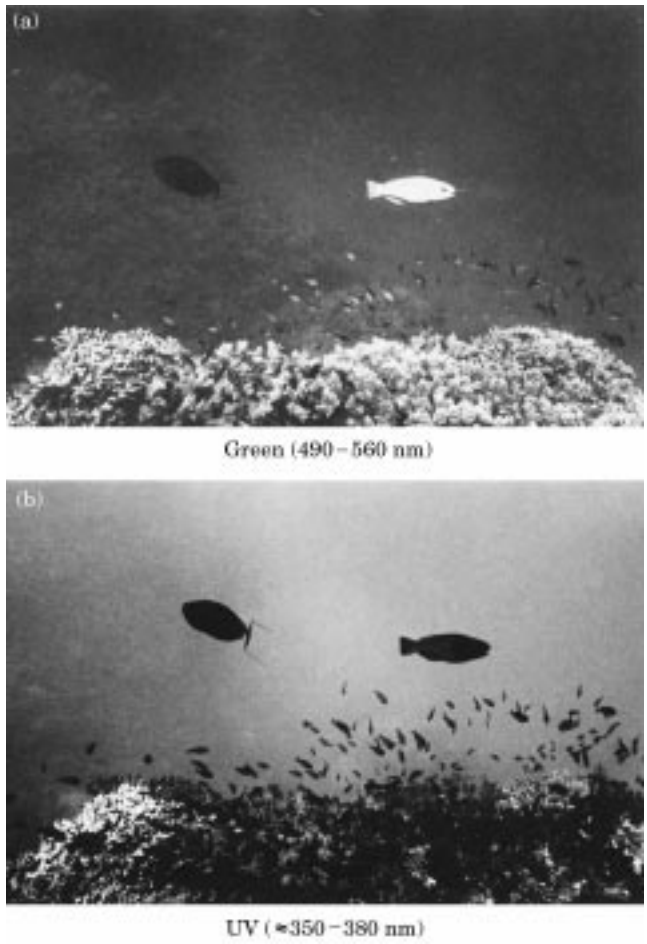

FIG. 8. Images taken simultaneously through (a) green-transmitting and (b) UV-transmitting filters, as in Fig. 7. The film used is Fuji Neopan 1600, and the site is near Yonge Reef, Great Barrier Reef, Australia at a depth of about 10 m. Note the strong colour contrast apparent in the green parrot fish (facing to the right), as well as the silhouetting of the other fishes in the image when viewed against the UV background space light.

the fact that broadcast signals are present. The reversal in brightness of body areas in *Gramma loreto* (Poey) (Fig. 6) could be used as a broadcast signal, depending on the contrast with the background.

(2) Displaying contrasting colours in the UV that are veiled quickly with distance might approximate private signalling. Thin, brightly reflecting lines could form an effective courtship display at short range that would all but disappear with distance and avoid reception by illegitimate receivers. The thin black lines on the head of *G. loreto* (Fig. 6) and its dorsal spot have much more contrast when viewed in the UV. This would give them some degree of privacy against fish that lack UV vision. In addition, the thin lines would be far less striking with distance granting universal privacy for all but the near at hand. This balance between conspicuousness for sexual and competitive display, while maintaining some crypsis is

known to be of primary concern to many animals including fish (Endler, 1991). Researchers should be aware that a lack of UV visualization equipment might render us blind to, or at least unaware of, important signals.

BREAKING OF CAMOUFLAGE OR CRYPSIS (COTT, 1940; FIGS 7 AND 8)

Adding shorter wavelengths to the detection array possessed by a predator poses even greater challenges for camouflage. In this case, UV vision would merely extend the wavelengths that an animal must match with its own pigments. Unfortunately, we may not appreciate an animal's choice of background without UV visualization capabilities: a UV-yellow fish might reject yellow backgrounds in favour of UV-yellow in order to match its body coloration best.

EXTENDED COLOUR VISION

While UV vision may have special uses like those suggested here, it also can play a more normal role in colour vision (see Fig. 5 and also Neumeyer, 1992; Coughlin & Hawryshyn, 1994) and may simply extend the spectral range within which fish see objects of interest.

CONCLUSIONS

At the very least, all fields of ichthyology in which coloration can be an important character must begin to consider short wavelength colours down through the UV-A. The ethologists must have some indication of the form of social and interspecific signals that can include a UV component and form a close range, if not semi-private, communication channel. Evolutionary biologists must consider selection pressure on coloration to include possibly a UV component. Even if the species of interest is shown to lack UV vision, interspecific selection might be present. Especially in clear shallow water habitats, at least some of the species in the community are highly likely to possess UV vision. Taxonomists should examine variability in the inclusion of UV reflectance in otherwise similar hues. A major task before us now is to identify particular biological situations such as plankton feeding and social communication in which UV vision might be of special significance to fishes.

This review resulted from a workshop at the Fifth Indo-Pacific Fish Conference in Noumea, New Caledonia, in November 1997, that was funded, in part, by the Department of the Navy Grant N62649-96-1-0013, issued by U.S. FISC YOKOSUKA to GSL. This material was supported by the National Science Foundation under Grant No. IBN-9413357 to TWC, and OCE-9810387 to GSL.

References

Andersson, S. & Amundsen, T. (1997). Ultraviolet colour vision and ornamentation in bluethroats. *Proceedings of the Royal Society of London B* **264,** 1587–1591.

Arikawa, K., Inokuma, K. & Eguchi, E. (1987). Pentochromatic visual system in a butterfly. *Naturwissenschaften* **74,** 297–298.

Avery, J. A., Bowmaker, J. K., Djamgoz, M. B. A. & Downing, J. E. G. (1983). Ultraviolet sensitive receptors in a freshwater fish. *Journal of Physiology (London)* **334,** 23.

Baker, K. S. & Smith, R. C. (1982). Spectral irradiance penetration in natural waters. In *The Role of Solar Ultraviolet Radiation in Marine Ecosystems* (Calkins, J., ed.), pp. 233–246. New York: Plenum Press.

Barlow, H. B. (1982). What causes trichromacy? A theoretical analysis using comb-filtered spectra. *Vision Research* **22,** 635–643.

Beatty, D. D. (1984). Visual pigments and the labile scotopic visual system of fish. *Vision Research* **24,** 1563–1573.

Bennett, A. T. D., Cuthill, I. C. & Norris, K. J. (1994). Sexual selection and the mismeasure of color. *American Naturalist* **144,** 848–860.

Bennett, A. T. D., Cuthill, I. C., Partridge, J. C. & Lunau, K. (1997). Ultraviolet plumage colors predict mate preferences in starlings. *Proceedings of the National Academy of Sciences of the USA* **94,** 8618–8621.

Blaxter, J. H. S. (1988). Sensory performance, behaviour, and ecology of fish. In *Sensory Biology of Aquatic Animals* (Atema, J., Fay, R. R., Popper, A. N. & Tavolga, W. N., eds), pp. 203–232. New York: Springer-Verlag.

Bowmaker, J. K. (1983). Trichromatic colour vision: why only three receptor channels? *Trends in NeuroSciences* **6,** 41–43.

Bowmaker, J. K. (1990). Visual pigments of fishes. In *The Visual System of Fishes* (Douglas, R. H. & Djamgoz, M. B. A., eds), pp. 81–107. London: Chapman & Hall.

Bowmaker, J. K. (1991). The evolution of vertebrate visual pigments and photoreceptors. In *Evolution of the Eye & Visual System* (Cronly-Dillon, J. R. & Gregory, R. L., eds), pp. 63–81. Boca Raton, FL: CRC Press, Inc.

Bowmaker, J. K. (1995). The visual pigments of fish. *Progress in Retinal and Eye Research* **15,** 1–31.

Bowmaker, J. K., Thorpe, A. & Douglas, R. H. (1991). Ultraviolet-sensitive cones in the goldfish. *Vision Research* **31,** 349–352.

Bridges, C. D. B. (1972). The rhodopsin–porphyropsin visual system. In *Handbook of Sensory Physiology, VII/1, Photochemistry of Vision* (Dartnall, H. J. A., ed.), pp. 471–480. New York: Springer-Verlag.

Browman, H. I. & Hawryshyn, C. W. (1992). Thyroxin induces a precocial loss of ultraviolet photosensitivity in rainbow trout (*Oncorhynchus mykiss*, Teleostei). *Vision Research* **32,** 2303–2312.

Browman, H. I., Novales-Flamarique, I. & Hawryshyn, C. W. (1994). Ultraviolet photoreception contributes to prey search behaviour in two species of zooplanktivorous fishes. *Journal of Experimental Biology* **186,** 187–198.

Burkhardt, D. (1983). Wavelength perception and colour vision. *Symposia of The Society for Experimental Biology* **36,** 371–397.

Chen, D. M. & Goldsmith, T. H. (1986). Four spectral classes of cone in the retinas of birds. *Journal of Comparative Physiology A* **159,** 473–479.

Chen, D. M., Collins, J. S. & Goldsmith, T. H. (1984). The ultraviolet receptor of bird retinas. *Science* **225,** 337–340.

Collier, R. & Zigman, S. (1987). The grey squirrel lens protects the retina from near-UV radiation damage. In *Degenerative Retinal Disorders. Clinical and Laboratory Investigations* (Hollyfield, J., ed.), pp. 571–585. New York: Liss.

Cott, H. B. (1940). *Adaptive Coloration in Animals*. London: Methuen.

Coughlin, D. & Hawryshyn, C. W. (1994). The contribution of ultraviolet and short-wavelength sensitive cone mechanisms to colour vision in rainbow trout. *Brain, Behaviour and Evolution* **43,** 219–232.

Cronin, T. W. & Frank, T. M. (1996). A short-wavelength photoreceptor class in a deep-sea shrimp. *Proceedings of the Royal Society of London B* **263,** 861–865.

Cronin, T. W., Marshall, N. J., Quinn, C. A. & King, C. A. (1994). Ultraviolet photoreception in mantis shrimp. *Vision Research* **34,** 1443–1452.

Denton, E. J. & Nicol, J. A. C. (1966). A survey of reflectivity in silvery teleosts. *Journal of the Marine Biological Association of the United Kingdom* **46,** 685–722.

Douglas, R. H. (1989). The spectral transmission of the lens and cornea of the brown trout (*Salmo trutta*) and goldfish (*Carassius auratus*)—effect of age and implications for ultraviolet vision. *Vision Research* **29,** 861–869.

Douglas, R. H. & McGuigan, C. M. (1989). The spectral transmission of freshwater teleost ocular media—an interspecific comparison and a guide to potential ultraviolet sensitivity. *Vision Research* **29,** 871–879.

Douglas, R. H. & Partridge, J. C. (1997). On the visual pigments of deep-sea fish. *Journal of Fish Biology* **50,** 68–85.

Douglas, R. H., Bowmaker, J. K. & Kunz, Y. W. (1995). Ultraviolet vision in fish. In *Seeing Contour and Colour* (Kulikowski, F. F., Dickinson, C. M. & Murray, I. F., eds), pp. 601–616. Oxford: Pergamon.

Dunlap, W. C., Williams, D. McB., Chalker, B. E. & Banaszak, A. T. (1989). Biochemical photoadaptation in vision: U.V.—absorbing pigments in fish eye tissues. *Comparative Biochemistry and Physiology* **93B,** 601–607.

Dunne, R. P. & Brown, B. F. (1996). Penetration of solar UVB radiation in shallow tropical waters and its potential biological effects on coral reefs: results from the central Indian Ocean and Adaman Sea. *Marine Ecology Progress Series* **144,** 109–118.

Eibl-Eibesfeldt, I. (1970). *Ethology: The Biology of Behaviour*. New York: Holt, Rinehart and Winston.

Endler, J. A. (1991). Variation in the appearance of guppy color patterns to guppies and their predators under different visual conditions. *Vision Research* **31,** 587–608.

Fleishman, L. J., Loew, E. R. & Leal, M. (1993). Ultraviolet vision in lizards. *Nature* **365,** 397.

Fox, D. L. (1953). *Animal Biochromes and Structural Colors: Physical, Chemical, Distributional & Physiological Features of Colored Bodies in the Animal World*. Berkeley: University of California Press.

Fox, H. M. & Vevers, G. (1960). *The Nature of Animal Colours*. London: Sidgwick and Jackson.

Frank, T. M. & Widder, E. A. (1996). UV light in the deep-sea: in situ measurements of downwelling irradiance in relation to the visual threshold sensitivity of UV-sensitive Crustaceans. *Marine and Freshwater Behaviour and Physiology* **27,** 189–197.

Goldsmith, T. H. (1990). Optimization, constraint, and history of the evolution of eyes. *Quarterly Review of Biology* **65,** 281–322.

Goldsmith, T. H. (1994). Ultraviolet receptors and color vision: evolutionary implications and a dissonance of paradigms. *Vision Research* **34,** 1479–1487.

Harosi, F. I. & Hashimoto, Y. (1983). Ultraviolet visual pigments in a vertebrate: a tetrachromatic cone system in the Dace. *Science* **222,** 1021–1023.

Hart, N. S., Partridge, J. C. & Cuthill, I. C. (1998). Visual pigments, oil droplets and cone photoreceptor distribution in the European starling (*Sturnus vulgaris*). *Journal of Experimental Biology* **201,** 1433–1466.

Hawryshyn, C. W. (1992). Polarization vision in fishes. *American Scientist* **80,** 164–175.

Hawryshyn, C. W. & Beauchamp, R. D. (1985). Ultraviolet photosensitivity in goldfish: an independent U.V. retinal mechanism. *Vision Research* **25,** 11–20.

Hawryshyn, C. W. & Bolger, A. (1991). Spatial orientation of rainbow trout: effects of the degree of polarization of the polarized light field. *Journal of Comparative Physiology A* **167,** 691–697.

Hawryshyn, C. W. & Harosi, F. I. (1991). Ultraviolet photoreception in carp: microspectrophotometry and behaviourally determined action spectra. *Vision Research* **31,** 567–576.

Hawryshyn, C. W. & McFarland, W. N. (1987). Cone photoreceptor mechanisms and the detection of polarized light in fish. *Journal of Comparative Physiology* **A160,** 459–465.

Hisatomi, O., Satoh, T., Barthel, L. K., Stenkamp, D. L., Raymond, P. A. & Tokunaga, F. (1996). Molecular cloning and characterization of the putative ultraviolet-sensitive visual pigment of goldfish. *Vision Research* **36,** 933–939.

Jacobs, G. H. (1992). Ultraviolet vision in vertebrates. *American Zoologist* **31,** 544–554.
Jerlov, N. G. (1968). *Optical Oceanography*. New York: Elsevier.
Jerlov, N. G. (1976). *Marine Optics*. Amsterdam: Elsevier.
Johnson, R. L., Grant, K. B., Zankel, T. C., Boehm, M. F., Merbs, S. L., Nathans, J. & Nakanishi, K. (1993). Cloning and expression of goldfish opsin sequences. *Biochemistry* **32,** 208–214.
Jokiel, P. L. (1980). Solar ultraviolet radiation and coral reef epifauna. *Science* **207,** 1069–1071.
Kasukawa, H., Oshima, N. & Fujii, R. (1987). Mechanism of light reflection in blue damselfish motile iridophore. *Zoological Science* **4,** 243–257.
Kennedy, D. & Milkman, R. D. (1956). Selective light absorption by the lenses of lower vertebrates, and its influence on spectral sensitivity. *Biological Bulletin* **111,** 375–386.
Kunz, Y. W., Wildenburg, G., Goodrigh, L. & Callaghan, E. (1994). The fate of ultraviolet receptors in the retina of the Atlantic salmon (*Salmo salar*). *Vision Research* **34,** 1375–1383.
Land, M. F. (1972). The physics and biology of animal reflectors. In *Progress in Biophysics & Molecular Biology* (Butler, J. A. V. & Noble, D., eds), Vol. 24, pp. 75–106. Oxford: Pergamon Press.
Larned, S. (1995). Effects of ultraviolet radiation and nitrogen enhancement on growth in the coral reef chlorophytes *Dictyosphaeria cavernosa* and *Dictyosphaeria versluysii*. In *Ultraviolet Radiation & Coral Reefs* (Gulko, D. & Jokiel, P. L., eds), pp. 181–191. Honolulu, Hawaii: Technical Report No. 41. Sea Grant Publication UNIHI-SEAGRANT-CR-95-03.
Loew, E. R. (1994). A third, ultraviolet-sensitive, visual pigment in the Tokay Gekko, *Gekko gekko*. *Vision Research* **34,** 1427–1432.
Loew, E. R. & McFarland, W. N. (1990). The underwater visual environment. In *The Visual System of Fish* (Douglas, R. H. & Djamgoz, M., eds), pp. 1–43. New York: Chapman & Hall.
Loew, E. R. & Wahl, C. M. (1991). A short-wavelength sensitive cone mechanism in juvenile yellow perch, *Perca flavescens*. *Vision Research* **31,** 353–360.
Loew, E. R., McFarland, W. N., Mills, E. & Hunter, D. (1993). A chromatic action spectrum for planktonic predation by juvenile yellow perch, *Perca flavescens*. *Canadian Journal of Zoology* **71,** 384–386.
Loew, E. R., McAlary, F. A. & McFarland, W. N. (1996). Ultraviolet sensitivity in the larvae of two species of marine atherinid fishes. In *Zooplankton Sensory Ecology & Physiology* (Lenz, P. H., Hartline, D. K., Purcell, J. E. & Macmillan, D. L., eds), pp. 195–209. Sydney: Gordon & Breach.
Lythgoe, J. N. (1979). *The Ecology of Vision*. Oxford: Clarendon Press.
Lythgoe, J. N. (1980). Vision in fishes: ecological adaptations. In *Environmental Physiology of Fishes* (Ali, M. A., ed.), pp. 431–445. London: Plenum Publishing.
Lythgoe, J. N., Muntz, W. R. A., Partridge, J. C., Shand, J. & Williams, D. M. (1994). The ecology of the visual pigments of snappers (Lutjanidae) on the Great Barrier Reef. *Journal of Comparative Physiology* **174,** 461–467.
MacNicol, E. F. (1986). A unifying presentation of photopigment spectra. *Vision Research* **26,** 1543–1556.
Mansfield, R. J. W. (1985). Primate photopigments and cone mechanisms. In *The Visual System* (Fein, A. & Levine, J. S., eds), pp. 89–106. New York: Alan R. Liss.
Marshall, N. J. (1996). Measuring colours around a coral reef. *Biophotonics International* **July/August,** 52–56.
McFarland, W. N. (1986). Light in the sea—correlations with behaviours of fishes and invertebrates. *American Zoologist* **26,** 389–401.
McFarland, W. N. & Loew, E. R. (1994). Ultraviolet visual pigments in marine fishes of the family Pomacentridae. *Vision Research* **34,** 1393–1396.
McFarland, W. N. & Munz, F. W. (1975*a*). The evolution of photic visual pigments in fishes. *Vision Research* **15,** 1071–1080.

McFarland, W. N. & Munz, F. W. (1975*b*). The photic environment of clear tropical seas during the day. *Vision Research* **15,** 1063–1070.
Merker, E. (1939). Die physiologische Leistung des Fischauges in kurzwelligen Licht. *Zoologische Jahrbucher Abteilung fur Allgemeine Zoologie und Physiologie der Tiere* **59,** 391–428.
Mollon, J. D. (1991). Uses and evolutionary origins of primate colour vision. In *Vision and Visual Dysfunction: Evolution of the Eye and Visual System* (Cronly-Dillon, J. R. & Gregory, R. L., eds), Vol. 2, pp. 306–319. London: Macmillan.
Muntz, W. R. A. (1973). Yellow filters and the absorption of light by the visual pigments of some Amazonian fishes. *Vision Research* **13,** 2235–2254.
Muntz, W. R. A. (1975). Behavioural studies of vision in a fish and possible relationships to the environment. In *Vision in Fish* (Ali, M. A., ed.), pp. 705–717. New York: Plenum.
Neumeyer, C. (1992). Tetrachromatic colour vision in goldfish: evidence from colour mixture experiments. *Journal of Comparative Physiology A* **171,** 639–649.
Novales Flamarique, I. & Hawryshyn, C. W. (1997). Is the use of underwater polarized light by fish restricted to crepuscular periods. *Vision Research* **37,** 975–989.
Osorio, D. & Vorobyev, M. (1996). Colour vision as an adaptation to frugivory in primates. *Proceedings of the Royal Society of London B* **263,** 593–599.
Palacios, A. G., Goldsmith, T. H. & Bernard, G. D. (1996). Sensitivity of cones from a cyprinid fish (*Danio aequipinnatus*) to ultraviolet and visible light. *Visual Neuroscience* **13,** 411–421.
Palacios, A. G., Varela, F. J., Srivastava, R. & Goldsmith, T. H. (1998). Spectral sensitivity of cones in the goldfish, *Carassius auratus*. *Vision Research* **38,** 2135–2146.
Parkyn, D. C. & Hawryshyn, C. W. (1993). Polarized-light sensitivity in rainbow trout (*Oncorhynchus mykiss*): characterization from multi-unit responses in the optic nerve. *Journal of Comparative Physiology A* **172,** 493–500.
Partridge, J. C. (1990). The colour sensitivity and vision of fishes. In *Light and Life in the Sea* (Herring, P. J., Campbell, A. K., Whitfield, M. & Maddock, L., eds), pp. 167–184. Cambridge: Cambridge University Press.
Partridge, J. C. & DeGrip, W. J. A. (1991). A new template for rhodopsin (vitamin A_1 based) visual pigments. *Vision Research* **31,** 619–630.
Partridge, J. C., Archer, S. N. & van Oostrum, J. (1992). Single and multiple visual pigments in deep-sea fishes. *Journal of the Marine Biological Association of the United Kingdom* **72,** 113–130.
Raymond, P. A., Barthel, L. K., Rounsifer, M. E., Sullivan, S. A. & Knight, J. K. (1993). Expression of rod and cone visual pigments in goldfish and zebrafish: a rhodopsin-like gene is expressed in cones. *Neuron* **10,** 1161–1174.
Raymond, P. A., Barthel, L. K. & Stenkamp, D. L. (1996). The zebrafish ultraviolet cone opsin reported previously is expressed in rods. *Investigative Ophthalmology and Visual Science* **37,** 948–950.
Robinson, J., Schmitt, E. A., Harosi, F. I., Reece, R. J. & Dowling, J. E. (1993). Zebrafish ultraviolet visual pigment: absorption spectrum, sequence, and localization. *Proceedings of the National Academy of Sciences of the USA* **90,** 6009–6012.
van Roessel, P., Palacios, A. G. & Goldsmith, T. H. (1997). Activity of long-wavelength cones under scotopic conditions in the cyprinid fish *Danio aequipinnatus*. *Journal of Comparative Physiology A* **181,** 493–500.
Silberglied, R. E. (1979). Communication in the ultraviolet. *Annual Review of Ecology and Systematics* **10,** 373–398.
Smith, R. C. & Baker, K. S. (1979). Penetration of UV-B and biologically effective dose-rates in natural waters. *Photochemistry and Photobiology* **29,** 311–323.
Tang, W. J. Y. (1993). Blot-affinity purification of antibodies. *Methods in Cell Biology* **37,** 95–104.
Thorpe, A., Douglas, R. H. & Truscott, R. J. W. (1993). Spectral transmission and short-wave absorbing pigments in the fish lens—I. Phylogenetic distribution and identity. *Vision Research* **33,** 289–300.

Townsend, C. H. (1929). Records of changes in colour among fishes. *Zoologica* **9,** 321–378.
Tsin, A. T. & Beatty, D. D. (1978). Goldfish rhodopsin: $P499_1$. *Vision Research* **18,** 1453–1455.
Tyler, J. E. & Smith, R. C. (1970). *Measurements of Spectral Irradiance Underwater*. New York: Gordon & Breach.
Vihtelic, T. S., Doro, C. J. & Hyde, D. R. (1999). Cloning and characterization of six different zebrafish photoreceptor opsin cDNAs and immunolocalization of their corresponding proteins. *Visual Neuroscience*, in press.
Whitmore, A. V. & Bowmaker, J. K. (1989). Seasonal variation in cone sensitivity and short-wave absorbing visual pigments in the rudd, *Scardinius erythrophthalmus*. *Journal of Comparative Physiology A* **166,** 103–115.
Zigman, S. (1993). Ocular light damage—yearly review. *Photochemistry and Photobiology* **57,** 489–492.
Zigman, S., Reddan, J., Schultz, J. B. & McDaniel, T. (1996). Structural and functional changes in catalase induced by near-UV radiation. *Photochemistry and Photobiology* **63,** 818–824.