Ocular media transmission of coral reef fish — can coral reef fish see ultraviolet light?

Ulrike E. Siebeck *, N. Justin Marshall

Department of Physiology, Vision, Touch and Hearing Research Center, University of Queensland, St. Lucia, Brisbane 4072, Australia

Abstract

Many coral reef fish are beautifully coloured and the reflectance spectra of their colour patterns may include UVa wavelengths (315–400 nm) that are largely invisible to the human eye (Losey, G. S., Cronin, T. W., Goldsmith, T. H., David, H., Marshall, N. J., & McFarland, W.N. (1999). The uv visual world of fishes: a review. *Journal of Fish Biology*, 54, 921–943; Marshall, N. J. & Oberwinkler, J. (1999). The colourful world of the mantis shrimp. *Nature*, 401, 873–874). Before the possible functional significance of UV patterns can be investigated, it is of course essential to establish whether coral reef fishes can see ultraviolet light. As a means of tackling this question, in this study the transmittance of the ocular media of 211 coral reef fish species was measured. It was found that the ocular media of 50.2% of the examined species strongly absorb light of wavelengths below 400 nm, which makes the perception of UV in these fish very unlikely. The remaining 49.8% of the species studied possess ocular media that do transmit UV light, making the perception of UV possible. © 2001 Elsevier Science Ltd. All rights reserved.

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1. Introduction

One of the first people to demonstrate an influence of UV radiation on the visual behaviour of animals was John Lubbock (Lord Avebury) who showed in 1888 that ants were sensitive to UV light (Lubbock, 1888). Since then UV sensitivity has been shown to exist in many animals including arthropods (von Frisch, 1953; Autrum & von Zwehl, 1964; Silberglied, 1979; Koehler, Agee, Leppla, & Patterson, 1987; Menzel, Steinmann, De Souza, & Backhaus, 1988; Muir, Thorne, & Kay, 1992; Cronin, Marshall, Quinn, & King, 1994), amphibians and reptiles (Govardovskii & Zueva, 1974; Arnold & Neumeyer, 1987; Perry & McNaughton, 1991; Fleishman, Loew, & Leal, 1993; Loew, Govardovskii, & Roehlich, 1996; Sillman, Govardovskii, Roehlich, Southard, & Loew, 1997), birds (Huth, 1972; Goldsmith, 1980; Chen, Collins, & Goldsmith, 1984; Palacios & Varela, 1992; Bennett, 1994) and mammals (Jacobs, Neitz, & Deegan, 1991; Jacobs, 1992).

UV sensitivity has also been shown for a variety of fish species. It was demonstrated with behavioural experiments in the goldfish (Neumeyer, 1985; Hawryshyn & Beauchamp, 1985), the rainbow trout (Hawryshyn, Arnold, Chaisson, & Martin, 1989; Browman, Novales-Flamarique, & Hawryshyn, 1994), and the roach (Douglas, 1986). Measurements of the cone photopigments revealed the existence of UV sensitive photoreceptors in the dace, the carp and a series of other freshwater fishes (Avery, Bowmaker, Djamgoz, & Downing, 1982; Harosi & Hashimoto 1983; Hawryshyn & Harosi, 1991).

Three methods are frequently used to assess UV sensitivity: microspectrophotometry (MSP), analysis of retinal potentials with electrophysiological methods, and behavioural experiments based on visual discrimination tasks. While the first two methods answer the question of whether or not a visual system is UV sensitive, the behavioural studies illuminate the possible functional significance of UV perception for the animal. In birds for instance, it has been shown that the perception of UV patterns can be an important factor in sexual selection (Maier, 1994; Bennett, Cuthill, Partridge, & Lunau, 1997). Some freshwater fish are also

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* Corresponding author. Tel.: +61-7-33653127; fax: +61-7-33654522.

E-mail address: u.siebeck@vthrc.uq.edu.au (U.E. Siebeck).

known to use UV in mate choice (Archer & Lythgoe, 1990). Fish may also utilise UV in other important aspects of life, such as feeding, as recently demonstrated for a number of species including reef fish (Loew, McFarland, Mills, & Hunter, 1993; McFarland & Loew, 1994; Browman et al., 1994; Job & Bellwood, 1996).

In common with birds (Finger & Burkhardt, 1994), many coral reef fish have elaborate UV patterns (Losey, Cronin, Goldsmith, David, Marshall, & McFarland, 1999; Marshall, 1999). Many of the markings that reflect UV are located on the face or the fins of the fish, body regions that are frequently presented during display behaviours such as courtship, suggesting a role of the UV patterns in social communication (Thresher, 1983). Therefore, one might predict that many reef fish, especially those with elaborate UV patterns, should be sensitive to ultraviolet light.

In water, the available spectrum of light changes with depth (McFarland & Munz, 1975; Jerlov, 1976). Long wavelengths as well as short wavelengths are more strongly absorbed, and short wavelength are more strongly scattered than the middle of the spectrum, so that light at depth is blue or blue–green (predominant wavelength: 475 nm for Jerlov I oceanic water; Jerlov, 1976). UV photons do still exist at depth however, and in clear water they may be useable for vision to several hundred meters (Frank & Widder, 1996).

Tropical coral reef fishes live in relatively shallow water in a bright light environment where the down-welling sunlight still contains relatively large amounts of ultraviolet light. As UV radiation is known to cause photo-oxidative damage to retinal tissues it may therefore be advantageous for coral reef fish to protect their visual tissues from such damage. There are many examples of animals including humans that possess filters in the cornea, lens or vitreous that absorb UV radiation before it reaches the sensitive retinal tissues (Zigman, 1971). UV filters are also believed to enhance image quality by reducing the effect of optical imperfections of the ocular media that cause chromatic aberration and scatter. Both chromatic aberration and scatter are strongest for short wavelengths (Lythgoe, 1979). Those animals, which do not block UV from reaching the retina, may still have a UV absorbing filter (macular pigment) in the retina itself (Nussbaum, Pruett, & Delori, 1981). If this is not the case they presumably cope with the damage by a rapid replacement of photoreceptor tissues (Cameron & Easter, 1995), or by other unknown protection mechanisms. Alternatively they may die before the damage has a major impact on their visual sensitivity.

Many diurnal fish are known to possess UV opaque lenses and some species also have corneas which absorb UV radiation (Orlov & Gamburtzeva, 1976; Gamburtseva, Gnyubkina, Kondrashev, & Orlov, 1980; Kondra-shev, Gamburtzeva, Gnjubkina, Orlov, & Pham, 1986; Douglas, Bowmaker, & Kunz, 1989). The pigment concentrations in some of these UV absorbing ocular media are so high that the corneas or lenses appear yellow (Muntz, 1973; for review of yellow ocular media see Heinermann, 1984). While prior to this study only very few tropical marine species had been examined other studies have investigated lens transmittance of freshwater fish and fish from cold marine environments (Douglas & McGuigan, 1989; Thorpe, Douglas, & Truscott, 1993; McFarland & Loew, 1994).

In this paper a study of the ocular media (cornea, vitreous and lens) of 211 tropical coral reef fish species will be presented and it will be shown that 49.8% block UV from reaching the retina. It will also be shown that there is generally no correlation between the possession of UV body patterns and the potential for UV vision.

2. Materials and methods

2.1. Materials

The fish were caught with hand nets and a barrier net around the Heron Island and Lizard Island Reefs (Great Barrier Reef, Australia) using SCUBA at a depth of 5–20 m. They were kept in aquaria of the Heron Island and Lizard Island Research Stations before being prepared for measurement. Prior to taking measurements of their ocular media, the fish were anaesthetised with MS222 and killed by decapitation. The eyes were enucleated immediately to avoid artefacts of tissue degradation (Douglas & McGuigan, 1989).

2.2. Transmission measurements (whole eye, lens and cornea)

For the measurement of the whole eye, a window was cut into the back of the eye and the eye then placed into a black velvet eye holder. Spectral transmission spectra (300–800 nm) were obtained using 'Sub-spec', a portable spectrophotometer (modified version of Oriel Instruments Intraspec IV system, described in Marshall, 1996). All samples were measured in air (Douglas & McGuigan, 1989). A 'Spectralon' white tablet was used as a 99% reflection standard. The instrument beam was aimed through the eye or the individual ocular media at the white tablet. Xenon illumination was provided with a camera flash with front UV filter removed. After measuring the whole eyes, the lenses and corneas were isolated, rinsed to remove traces of blood and vitreous, and then measured separately. Transmission spectra were normalised in respect to the transmission level at 700 nm (Douglas & McGuigan, 1989). The standard means of characterising ocular media transmission is to

determine the wavelength at which 50% of the maximal transmittance (T50) was reached (Douglas & McGuigan, 1989). This was done using a linear regression similar to the method of Partridge (1989). In cases where no single T50 value could be found (species with yellow corneas) the T25 and T75 were determined instead.

2.3. Comparison with integrating sphere

The ideal method for measuring the transmission of refractive or scattering media, such as those found in eyes, is to use an integrating sphere to collect all rays passing through the medium. The method of imaging a white standard through the ocular media is unorthodox, but has several advantages such as being able to visualise the beam path, as well as extreme rapidity post

	SUB T50 [nm]	INT T50 [nm]
1	400	401
2	426	430
3	408	410

Fig. 1. Comparison of transmission measurements taken with Sub-spec with the more conventional method of using an integrating sphere to test if using Sub-spec is a valid method. Both curves represent the means of six measurements (three measurements each of two eyes of each individual). Measurements of the whole eye transmission of three species were compared in this way, and the resulting T50 values are given for the two methods. While there is some difference in the shape of the curve approaching 100% transmission the T(50) values are very similar. SUB, Sub-spec; INT, integration sphere. 1, *Liza argentea*; 2, *Hemigymnus fasciatus*; 3, *Selenotoca multifasciata*.
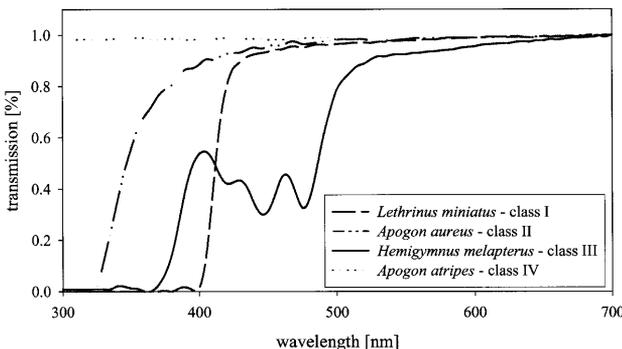
Fig. 2. Examples for the four different ocular media classes. Class I: whole eye transmission spectrum of *Lethrinus miniatus*, class II: lens transmission spectrum of *Apogon aureus*, class III: cornea transmission spectrum of *Hemigymnus melapterus* and class IV cornea transmission spectrum of *Apogon atripes*.

mortem. Therefore a calibration test was performed on three species (six eyes) to compare the sub-spec method with the integration sphere method on the same tissue. The results are very similar for both methods (Fig. 1), especially for the T50 values. It is believed this method of imaging the light path allows closer control of what is being measured and is particularly useful for the analysis of inhomogeneous corneas.

3. Results

3.1. Spectral transmission of corneas, lenses and whole eyes

The filter characteristics of the ocular media of most fish investigated here are generally similar to those of cut-off filters, as previously described for other species (Thorpe et al., 1993). Four classes of ocular media transmission spectra can be distinguished. The classes are characterised by the slope and the shape of the function (Fig. 2). Class I consists of curves with a very steep slope (< 30 nm between 0 and 100% transmission) and a sharp cut-off and can be found in whole eyes, corneas and lenses. Class II contains curves with a less steep slope and a gradual onset of the cut-off and can also be found in whole eyes, corneas and lenses. Class III is characterised by three intermediate maxima between maximal and minimal transmission and can be found in corneas and whole eyes. Class IV curves do not have a cut-off within the measured wavelength band, but transmit all wavelengths (300–700 nm) equally well (97–99%). Examples for this class can only be found in corneas.

The T50 values compared across all measured species (with transmission spectra class I and II) cover a large range, from 320 nm (*Apogon crassiceps*) to 437 nm (*Taeniura lymma*). The 75% maximal transmission of class III curves lie between 393 and 516 nm and the range between T25 and T75 values was often larger than 100 nm (Table 1, e.g. *Halichoeres melanurus*).

3.2. Which part of the ocular media is responsible for the transmission properties of the whole eyes?

To reach the retina, light must travel through vitreous humor as well as the lens and cornea. The ocular medium that absorbs at relatively longer wavelengths will determine the cut-off of the whole eye. Therefore this 'limiting' filter and the whole eye will have similar cut-offs. In this study, vitreous was not measured by itself. Comparisons of whole eye preparations, which contain vitreous humor, and isolated corneas or lenses, generally reveal little or no contribution to absorbance by the vitreous humor. There are two exceptions however, in which neither the lens nor the cornea accounts

Table 1
List of the 211 species with 50% maximal transmission values for whole eyes, corneas and lenses[a]

Order	Family	Species	Transmission			N
			Whole	Lens	Cornea	
Orectolobiformes	Orectolobidae – Wobbegongs	*Orectolobus ornatus*	II-403	II-367	II-398	2
Rajiformes	Rhinobatidae – Guitarfishes	*Rhinobatus typus*	I-408	I-408	II-400	6
	Dasyatidae – Stingrays	*Himantura fai*	I-415	I-418	–	1
		Pastinachus sephen	I-402	I-421	–	1
		Taeniura lymma	II-437	II-437	IV	1
		Urogymnus asperrimus	I-412	I-416	IV	1
Clupeiformes	Engraulidae – Anchovies	*Thryssa baelama*	I-405	I-400	II-352	1
Aulopiformes	Synodontidae – Lizardfishes	*Saurida gracilis*	I-410	I-408	II-367	1
Mugiliformes	Mugilidae – Mullets	*Crenimugil crenilabis*	II-366	II-370	–	1
		Mugil cephalus	I-409	I-409	II-373	1
		Liza argentea	I-400	I-397	II-382	1
Atheriniformes	Atherinidae – Hardyheads or Silversides	*Atherinomorus lacunosus*	II-358	II-358	II-316	1
	Hemiramphidae – Garfishes	*Hyporhamphus dussumieri*	II-354	II-350	II-355	1
		Hyporhamphus regularis ardelio	II-351	II-351	II-351	2
	Holocentridae – Squirrelfishes and Soldierfishes	*Myripristis murdjan*	II-369	II-355	–	1
		Sargocentron cornutum	II-393	II-389	II-354	2
		Sargocentron melanospilos	II-351	II-352	II-337	1
		Sargocentron spiniferum	II-380	II-352	II-375	1
Gasterosteiformes	Syngnathidae – Pipefishes	*Filicampus tigris*	I-429	I-432	II-354	1
	Aulostomidae – Trumpetfishes	*Aulostomus chinensis*	I-411	I-411	II-353	1
	Fistulariidae – Flutemouths	*Fistularia commersonii*	I-410	I-410	I-347	1
	Centriscidae – Razorfishes or Shrimpfishes	*Aeoliscus strigatus*	I-425	I-432	II-310	1
Scorpaeniformes	Scorpaenidae – Scorpionfishes	*Pterois antennata*	I-364	I-365	II-326	1
		Pterois volitans	I-360	II-360	IV	1
		Scorpaenopsis oxycephala	I-400	I-401	II-348	1
		Scorpaenopsis venosa	II-391	II-380	II-392	1
		Scorpaenodes guamensis	II-396	II-370	II-387	1
	Platycephalidae – Flatheads	*Thysanophrys arenicola*	II-398	II-396	II-357	2
Perciformes	Serranidae – Rockcods or Groupers	*Pseudanthias squamipinnis*	I-413	I-419	II-394	1
		Epinephelus coioides	I-402	I-402	II-340	1
		Epinephelus cyanopodus	I-410	I-409	II-356	1
		Epinephelus fasciatus	II-387	II-388	II-358	1
		Epinephelus quoyanus	I-402	I-404	II-352	2
		Cephalopholis boenak	I-404	I-403	II-345	5
		Cromileptes altivelis	II-406	I-400	II-421	1
		Plectropomus leopardus	I-414	I-411	II-349	2
	Pseudochromidae – Dottybacks and Eel Blennies	*Congrogadus subducens*	I-423	I-419	II-392	1
		Ogilbyina novaehollandiae	I-425	I-427	II-387	1
		Pseudochromis paccagnellae	I-427	I-430	II-369	1
		Pseudochromis fuscus	II-430	II-435	II-405	1
	Plesiopidae – Longfins	*Assessor macneilli*	II-407	II-411	–	1
	Priacanthidae – Bigeyes	*Priacanthus hamrur*	I-401	I-400	II-325	2
	Apogonidae – Cardinalfishes	*Apogon atripes*	II-362	II-365	IV	2
		Apogon aureus	II-347	II-351	IV	1
		Apogon bandanensis	II-353	II-351	–	1
		Apogon crassiceps	II-321	–	IV	1
		Apogon cyanosoma	II-349	II-352	IV	2
		Apogon doederleini	II-355	II-361	IV	2
		Apogon fraenatus	II-351	II-347	II-347	1
		Apogon fragilis	II-352	II-350	IV	6
		Apogon leptacanthus	II-349	II-354	IV	1
		Apogon sangiensis	II-349	–	II-324	1
		Cheilodipterus quinquelineatus	II-393	II-398	II-326	2
		Rhabdamia gracilis	II-371	II-367	–	1

Table 1 (*Continued*)

Order	Family	Species	Transmission			N
			Whole	Lens	Cornea	
	Echeneidae – Remoras	*Echeneis naucrates*	I-407	I-407	II-383	2
	Carangidae – Trevallies	*Alectes ciliaris*	I-407	I-406	II-383	1
		Elagatis bipinnulata	I-404	I-404	II-366	1
		Pseudocaranx dentex	I-405	I-405	II-384	2
		Selar boops	I-399	I-398	II-348	2
	Lutjanidae – Snappers	*Lutjanus bohar*	II-386	II-366	II-384	6
		Lutjanus carponotatus	I-395	I-397	I-376	3
		Lutjanus fulviflamma	I-388	I-384	I-374	2
		Lutjanus gibbus	II-370	II-370	II-367	1
		Lutjanus quinquelineatus	II-373	II-373	II-365	1
		Lutjanus russelli	II-381	II-381	II-381	1
	Caesionidae – Fusiliers	*Caesio cuning*	II-380	II-377	II-329	1
		Pterocaesio marri	II-378	II-377	II-372	3
	Gerreidae – Silver Biddies	*Gerres oyena*	I-391	I-392	II-334	4
	Haemulidae – Sweetlips	*Diagramma pictum*	II-378	II-365	II-353	1
		Plectorhinchus picus	I-394	I-397	–	1
	Lethrinidae – Emperors	*Gymnocranius audleyi*	I-416	I-415	II-382	1
		Lethrinus miniatus	I-410	I-408	II-387	3
		Lethrinus nebulosus	I-412	I-412	I-388	2
	Nemipteridae – Coral Breams	*Scolopsis bilineatus*	I-405	I-404	II-376	3
		Scolopsis margaritifer	I-406	I-406	II-383	2
		Scolopsis monogramma	I-412	I-412	II-356	1
	Mullidae – Goatfishes	*Parupeneus barberinoides*	–	II-350	–	1
		Parupeneus barberinus	II-352	II-356	II-350	1
		Parupeneus heptacanthus	II-335	II-341	II-322	1
		Parupeneus multifasciatus	II-350	II-345	IV	3
	Pempheridae – Sweepers	*Pempheris analis*	II-363	II-366	II-331	1
	Chaetodontidae – Butterflyfishes	*Chaetodon baronessa*	I-405	I-404	II-349	1
		Chaetodon citrinellus	I-404	I-405	II-357	1
		Chaetodon flavirostris	I-404	I-402	II-354	5
		Chaetodon melannotus	I-406	I-405	II-362	1
		Chaetodon ornatissimus	I-390	I-391	II-350	1
		Chaetodon oxycephalus	I-412	I-412	II-368	1
		Chaetodon pelewensis	I-376	I-377	II-353	1
		Chaetodon plebeius	I-407	I-407	II-364	1
		Chaetodon rainfordi	I-409	I-407	II-368	1
		Chaetodon trifascialis	I-381	I-381	II-370	1
		Chaetodon ulietensis	I-407	–	–	1
		Chaetodon unimaculatus	II-393	II-391	II-382	1
		Chelmon rostratus	I-409	I-408	II-352	1
		Coradion altivelis	I-399	I-396	II-348	1
		Heniochus acuminatus	II-382	II-377	II-377	1
		Heniochus chrysostomus	–	II-380	–	1
		Heniochus diphreutes	I-373	I-373	II-348	1
		Heniochus monocerus	I-378	I-374	II-374	3
		Heniochus singularius	I-396	I-394	II-369	1
		Heniochus varius	I-367	I-365	II-337	1
	Pomacanthidae – Angelfishes	*Centropyge bicolor*	I-406	I-407	I-369	3
		Chaetodontoplus meredithi	I-412	I-411	II-349	1
		Pomacanthus imperator	I-409	I-407	II-324	1
		Pomacanthus sexstriatus	I-409	I-408	II-379	1
		Pygoplites diacanthus	I-409	I-408	IV	1
	Teraponidae – Grunters	*Terapon jarbua*	I-377	I-375	II-352	1
	Pomacentridae – Damselfishes	*Pomacentrus* sp.	II-337	II-335	IV	1
		Abudefduf bengalensis	II-338	II-330	II-337	1
		Abudefduf whitleyi	II-342	II-343	II-336	2
		Amblyglyphidodon curacao	II-350	II-343	II-345	2
		Amblyglyphidodon leucogaster	II-352	II-350	II-348	1
		Amphiprion akindynos	II-362	II-358	II-349	2
		Amphiprion perideraion	II-370	II-380	II-364	1

Table 1 (*Continued*)

Order	Family	Species	Transmission			N
			Whole	Lens	Cornea	
		Chromis atripectoralis	II-348	II-340	II-352	1
		Chromis nitida	I-365	I-364	IV	1
		Dascyllus aruanus	II-331	II-328	II-333	1
		Dascyllus reticulatus	I-343	I-345	II-344	1
		Dischistodus prosopotaenia	II-355	II-350	II-350	1
		Dischistodus perspicillatus	II-387	I-355	II-387	1
		Neoglyphidodon melas	II-358	II-349	II-353	2
		Neopomacentrus azysron	II-330	II-324	IV	1
		Pomacentrus moluccensis	II-335	II-334	II-327	1
		Pomacentrus bankanensis	II-319	II-322	II-327	1
		Pomacentrus coelestis	–	II-336	–	2
		Pomacentrus chrysurus	II-331	II-332	II-320	1
		Pomacentrus wardi	II-365	II-341	–	1
		Premnas biaculeatus	II-345	II-350	II-354	1
		Stegastes apicalis	II-360	II-355	II-350	3
		Stegastes fasciolatus	II-328	II-332	II-324	1
	Labridae – Wrasses	*Anampses geographicus*	III-424–508	I-427	III-350–502	2
		Anampses neoguinaicus	III-428–480	I-425	III-387–480	1
		Bodianus diana (adult)	III-427–500	I-380	III-424–500	1
		Cheilinus chlorourus	III-430–500	I-429	III-350–520	1
		Cheilinus diagrammus	III-433–500	I-433	III-348–399	4
		Cheilinus trilobatus	III-425–502	I-427	III-383–492	1
		Choerodon cyanodus	III-390–495	II-383	III-390–493	2
		Choerodon fasciatus	III-396–493	I-397	III-387–500	3
		Choerodon venustus	II-402	I-376	II-399	3
		Cirrhilabrus punctatus (term.)	–	I-378	IV	1
		Coris gaimard (juv.)	–	I-430	III-347–393	1
		Epibulus insidiator (brown phase)	III-427–495	I-426	III-398–495	1
		Gomphosus varius (term)	III-425–492	I-433	III-348–445	1
		Halichoeres hortulanus (adult)	III-420–528	I-430	III-414–489	1
		Halichoeres melanurus (term)	III-444–509	I-426	III-390–509	1
		Halichoeres ornatissimus	III-424–515	I-426	III-392–513	1
		Halichoeres prosopeion	III-430–485	I-426	III-385–485	2
		Halichoeres trimaculatus	–	I-427	–	1
		Hemigymnus fasciatus	III-422–494	I-424	III-386–497	3
		Hemigymnus melapterus	III-422–493	I-422	III-342–515	8
		Hologymnosus doliatus	I-423	I-422	I-424	1
		Labroides dimidiatus	I-402	I-414	I-361	1
		Labropsis australis (term)	I-419	I-422	I-388	1
		Macropharyngodon choati	III-421–510	I-424	III-390–496	1
		Stethojulis strigiventer	III-416–483	I-422	III-413–480	1
		Thalassoma lunare	III-432–485	I-431	III-386–489	3
		Thalassoma lutescens	III-427–485	I-425	III-382–514	1
	Scaridae – Parrotfishes	*Scarus sp.*	I-423	I-421	II-388	1
		Scarus ghobban	–	I-424	–	1
		Scarus schlegeli	I-426	I-426	II-389	1
		Scarus psittacus term	I-429	I-428	II-391	2
		Chlorurus sordidus	I-426	I-425	II-388	5
	Pinguipedidae – Sandperches	*Parapercis cylindrica*	I-421	I-422	II-382	1
		Parapercis hexophtalma	I-422	I-420	II-388	1
	Blenniidae – Blennies	*Aspidontus taeniatus*	I-415	I-417	II-396	1
		Istiblennius edentulus	I-412	I-411	II-343	1
		Petroscirtes fallax	–	I-417	–	1
		Petroscirtes sp.	I-425	I-425	II-345	1
		Petroscirtes lupus	I-418	I-415	II-350	2
		Salarias fasciatus	I-415	I-413	II-365	3
	Gobiidae – Gobies	*Amblygobius phalaena*	I-408	I-412	IV	1
		Gobiodon citrinus	I-408	I-410	–	1
		Valenciennea longipinnis	I-413	I-413	II-376	4

Table 1 (*Continued*)

Order	Family	Species	Transmission			N
			Whole	Lens	Cornea	
	Microdesmidae – Wormfishes and Dartfishes	*Ptereleotris evides*	I-419	I-420	II-323	1
		Ptereleotris sp.	I-412	I-413	II-310	1
	Ephippidae – Batfishes	*Platax teira adult*	I-402	I-400	II-374	1
		Platax teira juv	I-394	I-394	II-369	1
	Siganidae – Rabbitfishes	*Siganus corallinus*	I-414	I-414	II-410	1
		Siganus doliatus	II-414	II-411	II-393	2
		Siganus fuscescens	I-408	I-408	II-387	2
	Zanclidae – Moorish Idol	*Zanclus cornutus*	I-409	I-410	II-349	1
	Acanthuridae – Surgeonfishes	*Acanthurus blochii*	I-410	I-410	II-387	1
		Acanthurus dussumieri	I-407	I-407	I-384	2
		Acanthurus nigrofuscus	I-412	I-411	I-384	1
		Ctenochaetus binotatus	I-409	I-410	II-381	1
		Ctenochaetus striatus	I-414	I-412	I-390	1
		Naso annulatus	II-391	II-386	II-397	1
		Naso brevirostris	I-398	I-386	I-397	4
		Naso lituratus	I-399	I-395	I-393	1
		Naso tuberosus	I-402	I-402	I-388	1
		Naso unicornis	I-410	I-411	II-393	2
		Naso vlamingii	I-392	I-383	I-396	2
		Zebrasoma scopas	I-413	I-409	II-390	1
		Zebrasoma veliferum	I-412	I-410	II-362	1
	Sphyraenidae – Barracudas	*Sphyraena flavicauda*	I-398	I-398	IV	2
		Sphyraena forsteri	I-404	I-402	IV	1
Tetraodontiformes	Balistidae – Triggerfishes	*Balistoides viridescens*	II-417	I-404	II-431	1
		Rhinecanthus aculeatus	III-395–495	I-400	III-399–495	5
		Sufflamen chrysopterus	III-405–494	I-404	III-396–504	3
		Sufflamen fraenatus	I-409	I-398	I-407	1
		Balistapus undulatus	III-405–488	I-407	III-400–493	1
	Monacanthidae – Leatherjackets	*Cantheschenia grandisquamis*	III-390–515	I-388	III-390–516	2
		Paraluteres prionurus	I-412	I-400	I-408	3
		Pseudomonacanthus peroni	II-407	II-389	II-400	1
	Ostraciidae – Boxfishes	*Ostracion cubicus*	II-393	II-397	II-341	3
	Tetraodontidae – Puffers	*Arothron* sp.	III-400–422	I-400	III-373–422	1
		Arothron hispidus	III-406–506	I-410	III-386–510	2
		Canthigaster macula	III-415–500	II-415	III-380–500	1
		Canthigaster valentini	III-405–500	I-407	III-370–500	1
		Canthigaster solandri = papua	III-400–501	I-400	III-350–505	1
		Tetractenos hamiltoni	I-414	I-416	II-396	1

[a] *N* is the number of animals measured. Transmission classes (I, II, III and IV) are given for corneas, lenses and whole eyes. The 'limiting' filter determines the class of the whole eyes, only in eyes with yellow corneas it is determined by the combination of the cornea and lens transmission (see Section 3).

for the T50 of the whole eye transmission (*Diagramma pictum* and *Neopomacentrus azysron*). Measurements of the vitreous for these two fish will be required to ascertain the true influence of the vitreous on the whole eye transmission characteristics.

3.2.1. Lenses

Lens transmission characteristics are invariably of class I or II. In 80% of all cases the lenses are the limiting filters of the whole eyes (Fig. 3A, B). Most other studies have in fact used only lens transmission as the parameter to compare ocular media transmission characteristics across species.

3.2.2. Corneas

Corneal transmission types can be found in all 4 classes (I–IV) identified. There were 13 instances in which the T50 value for corneas were at larger wavelengths than the T50 values of the lenses. In these fish the corneas are the limiting filters of the eye (Table 1). Examples of different corneal filters are as follows:

1. There are four examples in which corneas with transmission spectra class I determined the cut-off of the whole eye. The T50 values for those corneas are at 8–13 nm longer wavelengths than the T50 values of the lenses.
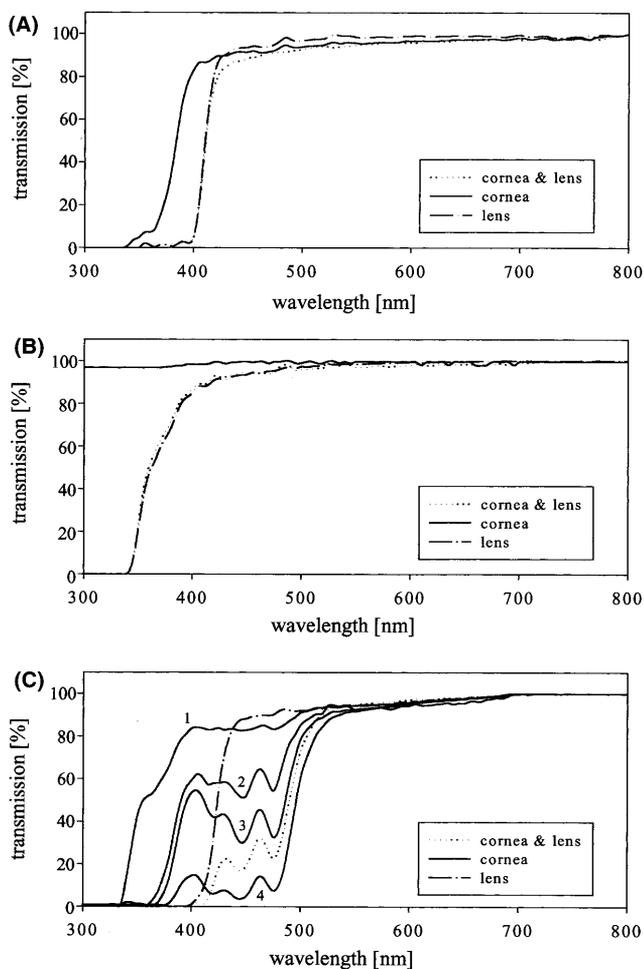
Fig. 3. Three typical combinations of the ocular media filters, the lens and the cornea and the resulting whole eye transmission. (A) *Acanthurus nigrofuscus*: cornea class I and lens class I. (B) *Apogon atripes*: cornea class IV and lens class II. (C) *Hemigymnus melapterus*: cornea class III and lens class I. Four example spectra are given for four areas of the cornea with different pigment densities (4 highest density–1 lowest density). The transmission of the whole eye was measured in the center of the eye.

2. Ten species have class II corneas that determine the cut-off of the whole eye.
3. Corneas of 31 species in four families (Labridae, Balistidae, Monacanthidae and Tetraodontidae) have complex cut-offs with three maxima between the maximal and minimal transmission (class III), indicative of carotenoid pigment (Moreland & Lythgoe, 1968; Bridges, 1969; Figs. 2 and 3C, Table 1). In most cases, the distribution of the pigment across the cornea was patchy, the highest density generally being found in the dorsal and ventral parts of the cornea, often decreasing towards the centre (typical for the families Balistidae, Monacanthidae and Tetraodontidae). Members of those families are able to retract the carotenoid pigment with decreasing light intensities and extend the pigment with increasing intensities (Fig. 4C). The light intensity therefore

determines the amount of pigment cover of the cornea, which is responsible for variable transmission properties of the whole eye. Five species were found with changeable yellow corneas, *R. aculeatus*, *S. chrysopterus* and *B. undulatus* (Balistidae), *C. grandisquamis* (Monacanthidae), and *A. hispidus* and *C. valentini* (Tetraodontidae). Wrasses (Labridae) had a more complex pattern of pigmentation with unpigmented areas embedded in highly pigmented areas (Fig. 4A, B). The pattern of pigmentation was constant within a species, but varied between species. The overall transmission of the whole eye is therefore variable and dependent on a combination of the pigmentation of the cornea and the lens transmission. While the densely pigmented areas of the cornea absorb relatively longer wavelengths than the lens, clear areas of the cornea transmit wavelengths that are subsequently absorbed by the lens (Fig. 3C).

4. There are 19 examples in which the cornea did not have a T50 value in the 300–800 nm wavelength band measured (class IV curves), (Fig. 3B).

3.3. Influence of lens size on the transmission characteristics

Age has been shown to have an influence on the transmission properties of the ocular media of fish, as the diameter of the lens continuously increases while the pigment production within the lens varies non–linearly (Thorpe & Douglas 1993). The ray, *Rhinobatus typus* is an example that showed an increase of the T50 values (405–414 nm) with increasing lens diameter (4.2–6.6 mm). The T50 values of *Lutjanus bohar*, however, showed almost no change with age (T50: 364–366 nm, lens diameter: 5–10.5 mm), (Fig. 5).
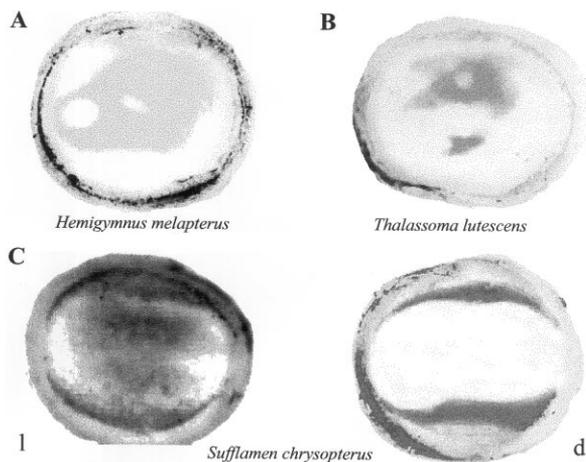
Fig. 4. Examples of yellow pigmented corneas. (A) *Hemigymnos melapterus*, (B) *Thalassoma lutescens* and (C) *Sufflamen chrysopterus* during light (l) and dark adaptation (d).
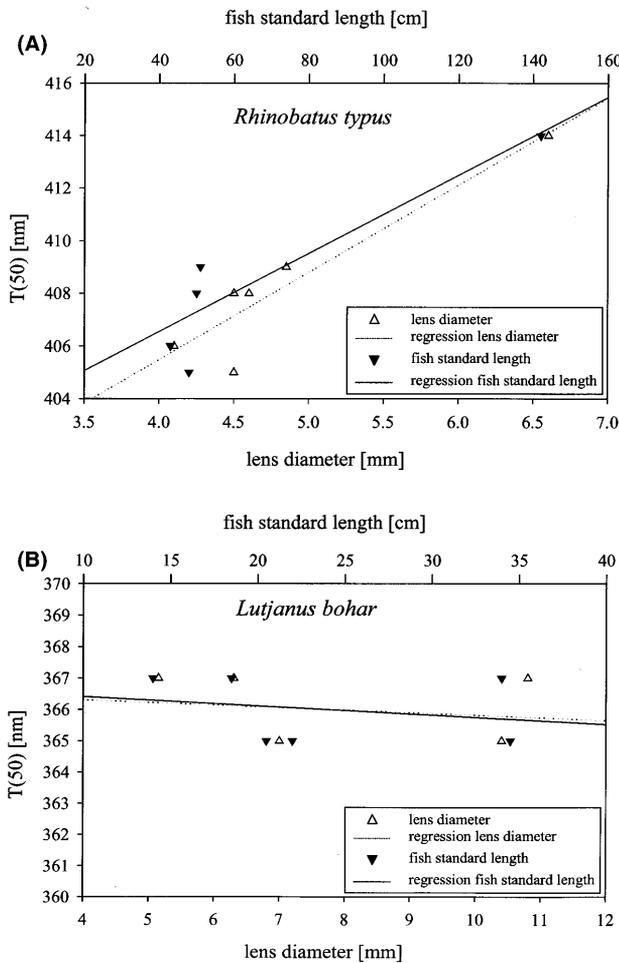
Fig. 5. Two examples for the influence of the diameter of the lens on its transmission. (A) Example where the transmission increases with increasing diameter of the lens (*Rhinobatus typus*). (B) Example where the transmission remains constant with increasing lens diameter (*Lutjanus bohar*). △, diameter; ▲, fish standard length.

3.4. Distribution of T50 values of 180 species

T50 values of 180 species were plotted as a convenient means of characterising spectral transmission. Where more than one specimen of the same species was measured the values of the largest individual were used. Unfortunately, although convenient, this method prohibits the inclusion of certain fish species. Those with yellow corneas could not be included, due to their lack of a single cut-off. Also species with class IV corneas could not be included in the transmission distribution of corneas, as their corneas have no T50 value within the measured wavelength band. The method also fails to distinguish between curves of the classes I and II. Within these limitations, however, the following trends are notable:

3.4.1. Whole eyes

The transmission distribution of whole eye T50 values appear to be roughly bimodal with clusters of similar T50 values around 350 and 410 nm (Fig. 6). The 410 nm cluster (84 species cut off between 400 and 420 nm) is much more prominent than the 350 nm cluster (27 species cut off between 340 and 360 nm). A total of 50.2% of the species have T50 values below 400 nm and 27.9% of the species transmit wavelengths to below 370 nm (Table 2A).

3.4.2. Lenses

The distribution of the lens T50 values is similar to that of the whole eyes (Fig. 6A) and is therefore also bimodal. This is because the lens is often the primary filtering element in transmission type I and II eyes.

3.4.3. Corneas

The T50 value distribution of the corneas appears to be trimodal with frequency peaks at 390 and 350 nm and possibly 330 nm. In comparison with the whole eye transmission distribution, the long wavelength peak is shifted towards shorter wavelengths, with most corneas cutting off at about 390 nm (Fig. 6B). Corneas generally cut off at lower T50 values than lenses (Fig. 6C).

3.5. Phylogenetic distribution of transmittance

3.5.1. Families with UV transmitting ocular media

A total of 108 species belonging to 22 families were found to have UV transmitting (T50 < 400 nm) ocular media (Fig. 7). Eight families include species with T50 values of less than 370 nm (Table 1). All species with UV transmitting ocular media in this study belong to the superorder Acanthopterygii. Species of the families Mullidae, Pomacentridae and Apogonidae had the lowest observed T50 values. The within family range of T50 values varied from family to family reaching values as large as 72 nm (Apogonidae). Transmission spectra in this group typically belong to class II (Fig. 2).

3.5.2. Families with examples of UV transmitters and also UV blockers

Seven families were found to have some species with, and others without, UV transmitting ocular media (Table 1). Species belonging to Chaetodontidae for example had T50 values from 367 up to 407 nm. Within the Chaetodontidae most UV transmitters were found in the genus *Heniochus*. Most species belonging to the genus *Chaetodon* had T50 values of more than 400 nm with four exceptions, *C. ornatissimus*, *C. pelewensis*, *C. trifascialis* and *C. unimaculatus*. Transmission spectra generally belonged to classes I and II. There are only two examples of species in this group with class III whole eye transmission spectra that transmitted wavelengths below 400 nm, *Cantheschenia grandisquamis* (Monacanthidae) and *Choerodon cyanodus* (Labridae).

3.5.3. Families with UV blocking ocular media

A total of 49.8% of all species were found to have T50 values between 401 and 460 nm (Table 2A). The within family variation is smaller than that for families with UV transmitting ocular media, and the transmission spectra generally belonged to class I, the five exceptions all having class II curves. All species with yellow pigmented corneas (class III curves), other than the two exceptions mentioned above, also belong to the group of UV blockers (Table 1).
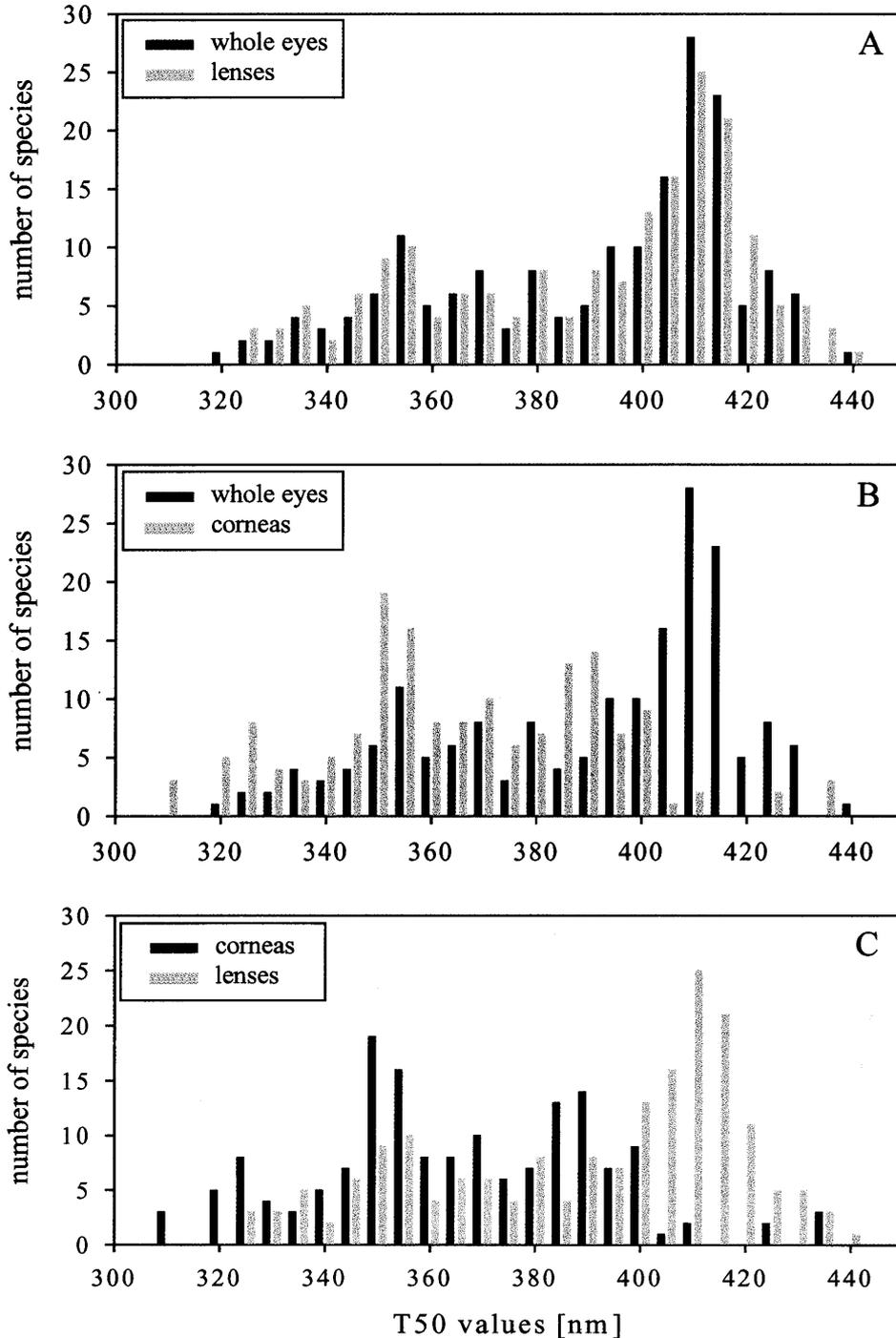
Fig. 6. Frequency distribution of the T50 values for whole eyes, corneas and lenses. Not included are yellow corneas as they do not have one clear cut-off. The shape of the distribution is very similar for whole eyes and lenses indicating that lenses are mostly responsible for the properties of the whole eyes (A). The distribution of the corneas seems to be trimodal while lens and whole eye distributions are bimodal (B, C). Compared to whole eye and lens T50 values, cornea T50 values are shifted towards lower wavelengths (B, C).

Table 2
Distribution of 50% maximal transmission values[a]

T50 (nm)	A T50 distribution All species are tropical marine (TM)			B T50 distribution for lenses only Various habitats (Thorpe et al., 1993)				C T50 distribution for freshwater fish lenses (Douglas & McGuigan, 1989)
	Whole eye (%)	Cornea (%)	Lens (%)	TM (%)	CM (%)	CF (%)	TF (%)	CF/TF (%)
300–340	8.8	25.5	7.9	0.0	32.7	50.0	25.0	44.0
341–370	19.1	38.0	20.0	6.0	7.3	25.0	30.0	6.0
371–400	22.3	28.0	23.7	50.0	30.9	12.5	22.5	16.0
401–430	47.9	6.5	45.0	44.0	27.3	12.5	7.5	10.0
431–460	1.9	2.0	3.4	0.0	1.8	0	15.0	24.0
N	205	96	207	16	55	8	40	50

[a] The species are divided into five groups with different T50 values. (A) Distributions of whole eyes, corneas and lenses of Great Barrier Reef fish. All fish were tropical marine (TM). (B) Lens transmission data from Thorpe and Douglas (1993). TM, tropical marine; CM, cold marine; CF, cold fresh water; TF, tropical fresh water. Freshwater species show a higher proportion of T50 values between 300 and 340 nm than marine species. (C) Lens transmission data of 50 freshwater species from Douglas and McGuigan (1989). A high proportion of the species have T50 values below 340 nm.
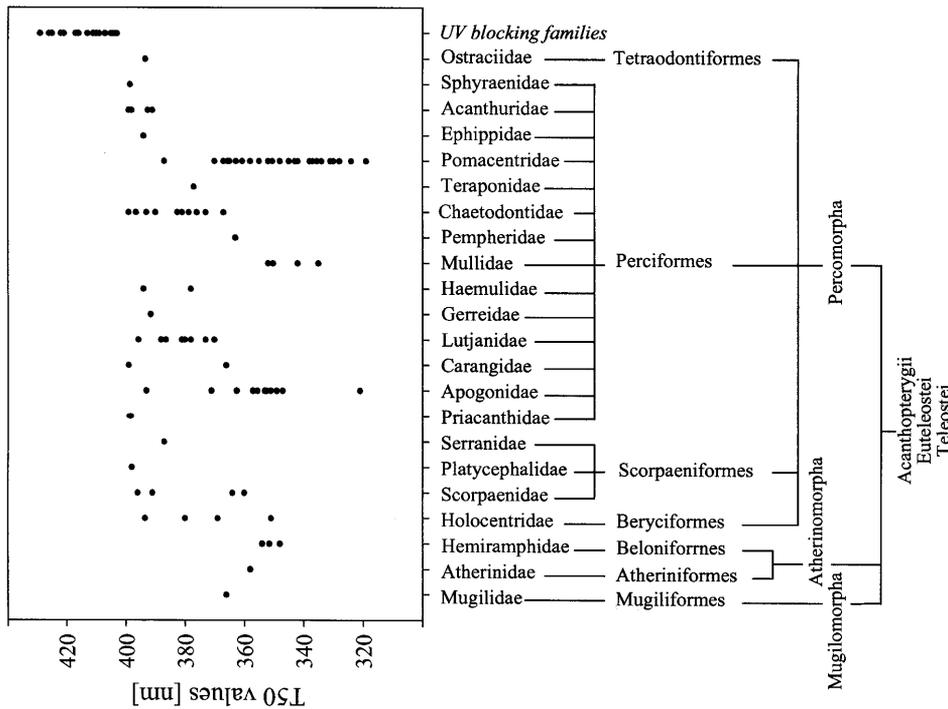
Fig. 7. Families with UV transparent ocular media. Species belonging to 22 families have T50 values of less than 400 nm. Each dot represents one species. The means of the families with UV blocking species are also included to demonstrate the continuity of the cut-off distribution.

4. Discussion

There are three important prerequisites for UV vision. In the habitat of the fish there has to be enough ultraviolet light for the detection by a visual system. The ultraviolet wavelengths have to reach the sensitive visual tissues which means that the ocular media of the fish have to transmit ultraviolet light. Finally, it is important to determine if the retina contains photoreceptors maximally sensitive to UV, or if UV sensitivity is achieved with β-band absorption of a photoreceptor maximally sensitive at longer wavelengths. In this study we have concentrated on the ocular media properties of coral reef fishes, with the aim of narrowing down the spectrum of species that might be sensitive to ultraviolet light.

4.1. Ultraviolet light in the habitat of the fish

Light is attenuated in water. The amount of attenuation depends on a variety of factors such as water type and depth. Long wavelengths and short wavelengths

are stronger attenuated than the middle part of the spectrum so that in several hundred meters depth the predominant wavelength is 475 nm (Jerlov, 1976). To estimate what depth ultraviolet light reaches the attenuation factors were used for different water types measured by Jerlov (1976), in combination with a surface irradiance measurement made on a sunny day on Heron Island (Fig. 8). An absolute visual threshold of 100 photons/cm^2 per s was assumed to estimate the maximum depths at which 350 nm light can still be detected (Denton, 1990). The calculation shows that at 20 m depth on a coral reef (Jerlov type 1) there are above threshold quantities of UV photons (350 nm). Jerlov attenuation coefficients are based on measurements made within the first few, relatively chlorophyll rich meters of water. Using them to estimate photons in depths to several hundred meters is likely to underestimate the actual amount of photons present at those

depths. The reason for that is that beyond the chlorophyll rich layer the attenuation is smaller as there are fewer particles that can scatter or absorb the light.

All the fish were caught at depths between 0 and 17 m, which can be assumed as an environment with above threshold quantities of ultraviolet photons at least to wavelengths as short as 350 nm.

4.2. Ocular media transmission

In general, the data presented here show that there is substantial variability in ocular media transmission both within and between families. T50 cut-offs can be found within a 200 nm wavelength band, between 320 and 430 nm, or in the case of carotenoid pigmentation T75 cut-offs of up to 520 nm. A total of 49.8% of the measured 211 species have ultraviolet absorbing ocular media. One should be careful though not to conclude from these results that fish with T50 values at 400 nm or even longer wavelengths are necessarily insensitive to UV light. There is at least one example in which UV sensitivity has been demonstrated in a gecko that has a lens with a T50 of 440 nm. However, the gecko lens possesses a transparent 'window' in the UV, which transmits wavelength around 350 nm (Ellingson, Fleishman, & Loew, 1995). To decide whether UV vision can be ruled out it is therefore important to check that there are no windows in the transmission of the lens, i.e. that the transmission of the lens equals 0% in the ultraviolet part of the spectrum.

4.2.1. Different cut-off classes and the chemical composition of filters

Based on the shape and the slope of the transmission spectra of corneas and lenses, four general classes were defined. The different classes and the high variability of T50 values (classes I and II), especially within class II, suggest that there is no single pigment that can explain all curves. So far the chemical composition of two distinct lens pigment groups has been identified: mycosporine compounds with absorbance maxima at 320, 330, 360 and 385 nm and 3-hydroxykynurenine with λ_{max} 370 nm (Thorpe & Douglas 1993). Interaction between pigment production and ocular media growth may also add to the high variability (Thorpe & Douglas 1993).

Class III curves show two cut-offs with three intermediate maxima at about 425, 440 and 480 nm. They are characteristic for corneas with visibly yellow pigmentation, which has been identified as carotenoid pigmentation (Muntz, 1973; Appleby & Muntz, 1979).

Finally, class IV curves describe corneal filters, which appear to have no pigmentation at all as they have no cut-offs within the measured wavelength band. The general classification used here is similar to that described in Douglas and McGuigan (1989). However,
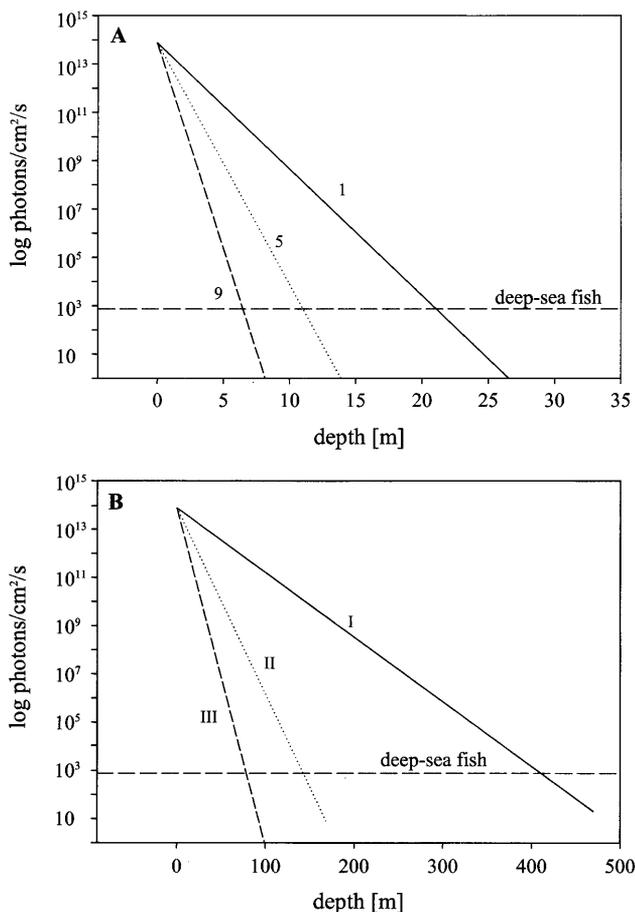
Fig. 8. Calculation of the maximum depths at which light with a wavelength of 350 nm can still be perceived in different water types (Jerlov, 1976). The depth will be slightly underestimated as we only have attenuation coefficients measured in the relatively turbid surface layer of each water type. More specific measurements of attenuation coefficients in deeper less turbid depths are needed, such as described in Frank and Widder (1996). The visual threshold for deep-sea fish is included as a guide although this will vary between species. (A) Jerlov coastal types 1, 5 and 9. (B) Jerlov oceanic types I, II and III.

some of their curves exhibit a secondary maximum around 320 nm, for which one has so few examples (*Pterocaesio marri*, *Lutjanus carponotatus* and *Pseudanthias squamipinnis*) that it was not used as a common classification.

4.2.2. Size or age and cut-off characteristics

As a result of the capture methods, most of the repeated measurements of the same species were done on fish of similar sizes and therefore had similar cut-offs. We did however manage to get a size range in some species and found two different patterns. Both patterns fit with the model proposed by Thorpe and Douglas (1993). The first pattern in which T50 increased with size matches phase 1 in Thorpe & Douglas' model and can be explained with a rapid pigment production that is relatively faster than the increase in lens diameter, so that the overall pigment concentration increases. The second pattern in which the T50 did not change with age fits phase 2 in the model and is achieved by a pigment production that is proportional to the increase in the lens diameter.

4.2.3. Yellow corneas

Thirty one species have noticeably yellow corneas. The distribution of the pigment in the cornea appears to be species specific, in accordance with the findings of Gamburtseva et al. (1980). The two types of yellow corneas, with and without changeable pigment distribution have also been described for a variety of other species (for review see Kondrashev et al., 1986; Gnyubkina & Levin, 1987; Gnyubkin, 1989). In species with the changeable type the pigment distribution depends on the light intensity. In bright light the pigment is extended into the central area of the cornea and in dim light it is retracted to the edges, presumably out of the light path (Gamburtseva et al., 1980). The process of fully retracting the pigment when a light adapted fish is transferred into darkness takes about 60 min (Appleby & Muntz, 1979).

Many labrid species investigated here show a constant, patchy distribution of the pigment across the whole cornea. Densely pigmented areas have a T75 of 520 nm while the clear spots sometimes transmit UV. The significance of the patchy pigment distribution is uncertain. The UV part of the light passing through clear patches in the cornea is absorbed in the lens. Where there is an aphakic aperture it may bypass the lens, in which case an unfocused UV signal may fall on part of the retina. A closer look at the receptor distribution in the retina is necessary to investigate the role of the patchy distribution.

Various authors have discussed the functions of yellow filters (Muntz, 1973; Appleby & Muntz, 1979; Gamburtseva et al., 1980; Kondrashev et al., 1986; Gnyubkina & Levin, 1987). They may be used to reduce chromatic aberration, which is highest for short wavelengths. They also reduce the effect of veiling light produced by scattering and help increase colour contrast in certain illumination conditions. As many mesopelagic fish also have yellow filters it has been proposed that in this particular niche their most likely function is to enhance bioluminescent signals (Clarke & Denton, 1962; Douglas, Partridge, & Marshall, 1998). One disadvantage of a yellow filter is the loss of sensitivity to short wavelengths and indeed an overall loss in sensitivity (Muntz, 1973; Appleby & Muntz, 1979; Gamburtseva et al., 1980; Kondrashev et al., 1986; Gnyubkina & Levin, 1987). However, this may not be a problem on a coral reef where plenty of light is available.

There are two strategies for surmounting the possible disadvantages associated with having yellow corneas. Many labrids and scarids stop their activity when the light intensities start to decrease and the sensitivity loss becomes apparent, and either bury themselves in sand or build cocoons. Species with movable pigment can retract the yellow pigment and thus they preserve their sensitivity and increase their wavelength spectrum, which may allow them to increase their active time (see Fig. 4C). Appleby and Muntz (1979) used the rate of pigment change and the rate at which the light levels change over time (in the tropics) during sunset and sunrise to estimate the time gained for a given visual efficiency. They found that there was no advantage at sunset as the pigment of *Tetraodon steindachneri* migrated as fast as the illumination decreased. At sunrise however 5–6 min were gained. During twilight predation is highest and 5–6 min lead to a considerable advantage of the species with occlusable yellow corneas over those without (Appleby & Muntz, 1979). More species will have to be investigated to get an estimate of the variability of the speed of the pigment movement and also to see if a natural day–night rhythm might yet lead to an advantage during sunset. This could be achieved by an early onset of pigment migration.

4.2.4. T50 distribution

The T50 value of each species has a characteristic position in the wavelength spectrum, between 300 and 440 nm. Generally, the spread of the T50 values across such a large wavelength range can be explained by either, effects of age, i.e. varying pigment densities, or differences in the chemical composition of the ocular media pigments. The variation with age alone, however, cannot explain the distribution patterns since lenses of different species with similar diameters often have completely different transmission characteristics (see also Douglas & McGuigan, 1989).

In similar studies Thorpe et al. (1993) (Table 2B) as well as Douglas and McGuigan (1989) (Table 2C) have measured the lens transmission of a variety of freshwater species as well as of some marine species. It is

Table 3
Proportion of species within four different T50 groups that have UV colouration[a]

T50 (nm)	Number of species with reflectance and transmission data	Proportion of species with UV reflecting patterns (%)
300–349	13	69
350–389	37	67
390–410	51	39
411–450	50	58

[a] N gives the number of species within each group for which one has both, reflectance and transmission data. The percentages show what proportion of the N species within each group has at least one colour with a UV component.

interesting that the distribution of the T50 values of tropical marine species differs from that of cold marine and freshwater species (Table 2). Freshwater (F) species and cold marine (CM) species tend to have a higher proportion of species (means of 76.6 and 70.9%, respectively) with ultraviolet transparent lenses than tropical marine (TM) species (mean of 54.8%). The difference in T50 values of CM/F and TM species is strongest in the category between 300 and 340 nm, with means of 32.7%/39.6% for CM/F and 3.95% for TM. Tropical marine species are exposed to intense radiation in the relatively shallow waters around coral reefs and are therefore probably more strongly effected by the danger of UV induced photo-oxidative damage and problems with image quality due to scatter than freshwater and cold marine fish. They may therefore gain advantages by having short wavelengths absorbing filters.

4.2.5. Phylogenetic distribution

All the fish species with UV transparent ocular media in this study belong to the superorder Acanthopterygii. Within this group, the order Perciformes was found to contain most of the UV transmitting species. At the same time perciforme species, which form the largest order within teleosts, also show the highest degree of variation. Some have T50 values as low as 320 nm, whilst others have values as high as 430 nm and still others have yellow corneas. The highest number of different lens pigments isolated in any order (Thorpe et al., 1993) matches this high variability in ocular media transmission. Species belonging to the orders Atheriniformes, Scorpaeniformes and Tetraodontiformes in comparison showed hardly any variation in ocular media transmission. Both Atheriniformes and Scorpaeniformes only contain species with UV transmitting ocular media, while Tetraodontiformes mostly cut-off around 400 nm ('clear' corneas) and between 400 and 500 nm (yellow corneas). None of the species of the orders Orectolobiformes or Rajiformes had UV transmitting ocular media in the study. Within the Rajiformes five species of the two

families, Rhinobatidae and Dasyatidae, were measured. The T50 values varied between 402 and 437 nm. In a different study, rajiforme species (family Rajidae) were found not to have any lens pigments at all (Thorpe & Douglas, 1993). It appears that the order Rajiformes is also quite diverse.

Within the perciforme order the within family variation was very small. There are only a few families, such as Serranidae, Chaetodontidae and Acanthuridae that show high diversity. Species belonging to the family Serranidae all had T50 values of around 405 nm with only one exception, *Epinephelus fasciatus* with a T50 of 387 nm.

4.2.6. Relationship between UV transmission and UV colouration

UV transmission does not automatically mean UV colouration. Reflectance data exists for 151 species of the 212 species described in this paper (Losey et al., 1999; Marshall, 1999). Table 3 shows the relationship between the UV transmittance of the ocular media with the occurrence of at least one UV reflecting colour on the body of the fish. About a third of the measured species transmit UV but do not have UV colouration.

UV colouration does not automatically mean UV transmission. More than half of the species with T50 values larger than 411 nm have UV colour patterns (Table 3). Assuming that those species cannot see the UV component of their own patterns one can only speculate why they might have UV patterns. UV patterns may be part of a camouflage strategy 'aimed' at the visual systems of other UV seeing fish. Fish may be UV sensitive in early life stages and lose that ability later in their lives, as shown for salmonid fishes (Hawryshyn et al., 1989). Alternatively UV colouration might not serve any specific function at all, but just be a by-product of the way some of the colours are constructed.

4.3. UV sensitive photoreceptors

If the UV wavelengths are not absorbed before they reach the sensitive tissues there are two different ways that UV sensitivity can be achieved. A receptor can either have its maximal sensitivity (α-peak) in the UV. Alternatively a receptor maximally sensitive to longer wavelengths can achieve UV sensitivity through absorption of UV wavelengths within its β-band (Dartnall & Lythgoe, 1965). There are some species for which the photoreceptor sensitivities have been measured that demonstrate both possibilities. McFarland and Loew (1994) found a photoreceptor with a λ_{max} of 360 nm in three species of Pomacentrids and Shand (1993) found a pigment with a λ_{max} of 400 nm (β-band in the UV) in the goatfish, *Upeneus tragula*.

We only have ocular media data for one of their species, *P. coelestis*, which has a T50 of 360 nm, but all

other species that were measured in the families Pomacentridae and Mullidae also had UV transparent ocular media. It is therefore possible that pomacentrids and mullids are generally sensitive to ultraviolet wavelengths. We have also found UV transmitting ocular media in other families, such as Apogonidae, Holocentridae, Lutjanidae and Hemiramphidae. These results make a search for UV receptors in more pomacentrid and mullid species as well as in species of the other families with UV transmitting ocular media promising.

5. Summary and conclusion

It has been shown that 50.2% of the investigated 211 species have UV transparent ocular media. A total of 49.8% of the investigated species block ultraviolet light and it is therefore unlikely that they have ultraviolet vision. In most cases the lenses are the limiting filters of the whole eyes. A combination of cornea and lens determines the transmission property of the whole eyes when the corneas contain carotenoid pigmentation. The distribution of the carotenoid pigment is always patchy and the individual patterns seem to be species dependent. There are two different types of yellow pigmented corneas. Labridae have constant pigmentation patterns whereas Balistidae, Monacanthidae and Tetraodontidae have variable pigmentation dependent on the illumination intensity. Many coral reef fish have colours that reflect ultraviolet light, but not all of them also have ultraviolet light transparent ocular media. Therefore ultraviolet colouration does not automatically mean ultraviolet vision.

The knowledge of the ocular media transmission by itself is not enough to conclude that an animal can see ultraviolet wavelengths as there may still be other absorbing filters in the light path. Examples of such filters are oildroplets in birds (Hart, Partridge, & Cuthill, 1998) or macular pigment in humans (Nussbaum et al., 1981). If there are no such filters then UV sensitivity can either be achieved with a photoreceptor maximally sensitive to UV, or with the β-band of a long wavelength photoreceptor. To determine between the possibilities MSP measurements, or behavioural experiments are needed.

It can be concluded, however, that it is very unlikely for species with UV absorbing ocular media (that have no windows in the UV) to have ultraviolet vision. So this study has achieved to narrow down the field of species with possible ultraviolet vision.

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