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An Anatomical Study of the Visual Capabilities of the Green Turtle, *Chelonia mydas*

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Several aspects of vision in juvenile and adult Green Turtles (*Chelonia mydas*) are examined, with special reference to retinal anatomy such as oil droplet topography, transmission electron microscopy of photoreceptors, spectral transmission measurements of the ocular media (cornea, lens, and vitreous humor), and measurements of focal length and optical sensitivity. A detailed study of the distribution of the different color classes of oil droplets shows that all oil droplets are found in high concentrations (>1000 mm^{-2}) in the central/temporal parts of the retina. Red oil droplets were the largest, followed by yellow and clear. Oil droplet size varied in different parts of the retina. On average, red oil droplets were found in fewer numbers compared to yellow and clear oil droplets. Two types of clear oil droplets were identified: those that fluoresced under UV illumination and those that did not. We found that the majority (78.5%) of colorless oil droplets fluoresced when viewed under UV light. Spectral transmission measurements of the ocular media show that wavelengths to approximately 325 nm are transmitted. This may suggest ultraviolet (UV) vision in Green Turtles. The optical sensitivity of the Green Turtle eye was relatively low, suggesting an adaptation to high light intensities commonly experienced by this species.

GREEN Turtles (*Chelonia mydas*) have large breeding colonies on mainland shores and islands in tropical and subtropical oceans (Pritchard, 1997). *Chelonia mydas*, as well as many other sea turtles, are listed as endangered or vulnerable species, and it is mostly man-made impacts that are to blame for the drastic decrease in sea turtle populations worldwide (Lutcavage et al., 1997). There is ample evidence to suggest that marine turtles rely heavily on vision during the various stages of their lives (Limpus, 1971; Salmon et al., 1992; Lohmann et al., 1997), and it is perhaps not surprising that juvenile and adult Green Turtles are often caught as by-catch in long line fisheries (Hays et al., 2003; Carreras et al., 2004; Lewison et al., 2004), presumably being visually attracted by long lining equipment.

Little is known about the visual abilities of sea turtles, which is in part due to the fact that research on these animals is limited for conservation reasons. However, despite the difficulties involved in working with sea turtles, a number of important studies have been conducted. For instance, it has been shown that vision is a crucial sense that allows sea turtle hatchlings to find the ocean after hatching on the beach (Ehrenfeld and Carr, 1967; Mrosovsky and Shettleworth, 1968; Lohmann et al., 1997). Optics and accommodation of sea turtle eyes have been investigated (Ehrenfeld and Koch, 1967; Northmore and Granda, 1991) although the accommodative mechanism is still unknown. Morphological studies have shown that the retina of *C. mydas* and *Caretta caretta* is duplex in nature, containing rods and cones (Liebman and Granda, 1971; Bartol and Musick, 2001). The cones and ganglion cells of *C. mydas* and *C. caretta* are found in high concentrations in a horizontal visual streak, providing the animal with increased spatial resolving power along its visual horizon (Oliver et al., 2000; Bartol and Musick, 2001).

Microspectrophotometry has shown that sea turtles have the potential for color vision, since cone receptors with different visual pigments have been found (Liebman and Granda, 1971). Another feature indicating the importance of wavelength discrimination is the presence of colored oil droplets in the cone photoreceptors of sea turtles. Oil droplets are spherical organelles with high refractive properties. They are located between the inner and outer segments of cones, so that light passes through the oil droplets before it enters the cone outer segment. Most oil droplets contain carotenoid pigments (Liebman and Granda, 1975) and the color of oil droplets may vary from species to species.

TABLE 1. SIZE, APPROXIMATE AGE, AND SEX OF TURTLES USED IN THIS STUDY (DATA KINDLY PROVIDED BY K. ARTHUR, UNIVERSITY OF QUEENSLAND). Also shown for each turtle is what aspect of vision was studied. The number of each turtle is referred to in the corresponding results section.

Turtle number	Carapace length (cm)	Sex	Age (years)	Use of eye (RE, right eye; LE, left eye)
1	78	F	30–40	RE: oil droplet topography map (brightfield illumination); LE: other
2	47.2	M	10–30	LE: Transmission electron microscopy
3	46	F	10–30	RE: other; LE: Transmission electron microscopy; both lenses laser ray tracing
4	45	F	10–30	RE: other; LE: oil droplet map (white light)
5	43.7	F	20–30	RE: Spectral transmission of ocular media; LE: oil droplet topography map (brightfield illumination) + fluorescent oil droplet map
6	41	F	10–30	RE and LE: Spectral transmission of ocular media
7	40	F	10–30	Both lenses laser ray tracing

Freshwater turtles, *P. scripta elegans*, have red, orange-yellow, and colorless oil droplets, while those of Green Turtles, *C. mydas*, are described as orange, yellow, and colorless (Granda and Haden, 1970; Liebman and Granda, 1975; Ohtsuka, 1985). In a study of oil droplets in *Pseudemys*, Ohtsuka (1984) and Kolb and Jones (1987) found that colorless oil droplets could be subdivided into two classes: those that fluoresced under ultraviolet light and those that did not. Except for rods and the accessory members of double cones, all cones contain oil droplets (Walls, 1942; Liebman and Granda, 1971). It is generally believed that oil droplets shift the wavelengths available for absorption by the visual pigment towards the red end of the spectrum (Granda and O'Shea, 1972; Neumeyer and Jäger, 1985), which may enhance the detection of contrast by absorbing shorter wavelengths (such as blue light) more than longer wavelengths (such as red light). Vorobyev (2003) calculated that oil droplets reduce the overlap between photoreceptor spectral sensitivities and thereby increase the number of object colors that could be perceived by the animal. Blue light scatters more than red light, and the absorption properties of oil droplets may also reduce the effects of scatter and glare in the environment (Walls and Judd, 1933).

The objective of this study is to fill a number of the gaps in our knowledge about sea turtle vision and increase understanding of the visual capabilities of these animals. Here we describe aspects of vision of juvenile and adult Green Turtles, with special reference to oil droplet topography and photoreceptor anatomy. We also present the first spectral transmission measurements of the cornea, lens, and vitreous humor of the eye of the Green Turtle and suggest that these animals may have ultraviolet vision.

MATERIALS AND METHODS

The eyes of Green Turtles were collected from animals that had to be euthanized owing to disease or injury. The decision to euthanize animals was made by authorized personnel of Queensland Parks and Wildlife Services, Environmental Protection Agency (EPA permit WITK02629204). Turtles were euthanized by Veterinarians of the University of Queensland using an injection of Lethabarb (10–30 ml depending on the size of the animal). Table 1 shows a summary of the size, approximate age, and sex of the turtles that were used in this study and indicates how specimens were utilized.

Dissection.—Dorsal and nasal orientation slits were made to ensure that the orientation of the eyes in the head could be determined throughout the dissection, and both eyes were removed from the head. All dissections were made in 0.1 M phosphate buffer (pH 7.2). From each eye the cornea, lens, and a small amount of vitreous humor were removed for spectral transmission measurements. The entire retina was then carefully removed from the cartilaginous eye cup and investigated without fixation in order to preserve the coloration of the oil droplets. In most eyes, the pigment epithelium detached from the retina during dissection, otherwise remains of the pigment epithelium were brushed off gently with a delicate paint brush. The retina was then flat-mounted on a microscope slide with the photoreceptor layer pointing upwards. Spacers were placed around the retina to prevent the coverslip from pressing onto the retina, and the tissue was surrounded with glycerol before covering and sealing with nail polish. For each retina, approximately 70 areas were photographed using a digital camera (Spot Camera, Diagnostic Instruments Inc.) attached to a light

microscope (Zeiss Axioscope) equipped with epifluorescence. The microscope light source (Mercury, Zeiss) provided the UV waveband, which caused fluorescence of some clear oil droplets. The brightest autofluorescence was excited using a band pass filter (365 ± 12.5 nm) and measured using a long pass filter (400 nm).

Retinal topography maps were created using the rulers of the microscope stage. The rulers gave two-dimensional coordinates that were recorded on graph paper. Data were collected from prints where oil droplets were counted in 200 μm^2 areas. From these counts we extrapolated the total number of oil droplets per mm^2. Oil droplet diameters were measured using ImageJ software (National Institutes of Health, NIH).

Spectral transmission of ocular media.—The cornea, lens, and vitreous humor were dissected from the eye and placed on a piece of black plastic sheeting held by a clamp. The sheet had an approximately 3-mm diameter hole cut into it, above which the specimens were placed. Spectral transmission measurements (300–800 nm) were made using a fiber optic spectrometer (S-2000, Ocean Optics Inc., Florida) and a pulsed xenon light source (220–750 nm; PX-2, Ocean Optics). Two fiber optic cables (1-mm sampling diameter) were aligned so that light emitted from the illuminating fiber entered the measuring fiber. In this way the spectral transmission characteristics of material placed into the light beam could be determined. The measuring fiber was aligned so that it touched the material. All measurements were made in a dark room to prevent the influence of stray light. The fiber optic cables were held by a small stage, enabling fine control over the positioning of the cables.

Transmission electron microscopy (TEM).—For a closer investigation of photoreceptor anatomy, four retinae were prepared for TEM. Following dissection, five areas of the retina (dorsal, ventral, nasal, temporal, and central) were removed and immersed in fixative (0.25% glutaraldehyde, 4% paraformaldehyde in 0.1 M phosphate buffer) for a minimum of two hours. They were then immersed in a solution of 2% osmium tetroxide for two hours, followed by thorough washing in phosphate buffer and dehydration in a graded ethanol series. Specimens were transferred to 100% acetone (two changes) for 30 minutes and were then left overnight in a solution of Spurr's resin (TAAB) and acetone (50:50). They were embedded in Spurr's resin and transverse sections (gold sections; 90–150 nm thickness) were cut on a Reichert Jung Ultracut microtome and viewed on a JEOL JEM 1010 Transmission Electron Microscope. In order to test for regional variations of oil droplet size and cone outer segment dimensions, we measured between 15 and 20 cone cells in each of the five areas of the retina.

Focal length measurements.—Freshly excised lenses were measured in a custom-built lens tracing setup. The lens was placed in saline solution with a small quantity of a polymer solution (1 μm Polystyrene Microparticle, G Kisker Biotech) added. The beam of a laser pointer (532 nm, Leadlight Technology, Inc.) was moved horizontally through the lens while filming the lens from above using a digital camera (Sony DCR-TRV50E). Individual frames of the resulting video clip were overlayed in Adobe Photoshop. In the composite image the focal length was measured as the distance from the center of the lens to the point where the laser beam crossed.

Optical sensitivity.—A measure of the sensitivity of an eye to light of an extended source is given by the optical sensitivity which considers both the optical features of the eye and the light absorption of individual photoreceptors (Land, 1981). Optical sensitivity (S) is given by:

$$S\ (\mu m^2\ sr) = (\pi/4)^2 \times A^2 \times (d/f)^2 \times F$$

where A is the diameter of the circular aperture (pupil), d the diameter of the photoreceptor, f the focal length, and F the fraction of incident light absorbed by each photoreceptor. In this study, optical sensitivity was calculated for Turtle 3 (Table 1) using the dimensions of the cone outer segments measured from the electron microscopy sections, and the focal length obtained from the lens tracing. The aperture (pupil diameter) in Green Turtles was estimated to be between 40% and 66% of the lens diameter (concluded from Northmore and Granda, 1991). The fraction of incident light absorbed by the photoreceptor (F) can be calculated for both white light ($F_{\text{white light}} = kl/(2.3 + kl)$; Warrant and Nilsson, 1998) and monochromatic light ($F_{kmax} = 1 - e^{-kl}$; Land, 1981), where l is the length of the photoreceptor outer segment. The value for the photoreceptor absorbance coefficient (k) was estimated at 0.03 from data available on bony fishes (Partridge, 1990). Since the dimensions of the outer segments varied within the different parts of the retina, we chose average measured values for the optical sensitivity calculation. Although we did not take shrinkage into account when calculating optical sensitivity, considering that lungfish retinae shrink by 5%

during TEM preparation (Bailes et al., 2006), this should not impair our results.

Results

Oil droplet size and distribution.—We found that all types of oil droplets (red/orange, yellow, and clear) were present both in juvenile and adult animals (Fig. 1A). There was a distinct topography of oil droplet density in the retina of Green Turtles (Fig. 1B). Most oil droplets, irrespective of color, were found in the central/temporal parts of the retina (>1000 mm^{-2}). In total, oil droplet maps of three different turtle retinae (Turtles 1, 4, and 5) were constructed and the results were very similar.

We were able to map the fluorescent oil droplets throughout the retina of a juvenile animal (Turtle 5) and found that the majority (78.5%, s.e. 2.2, $n = 17$) of clear oil droplets fluoresced when viewed under UV light (Fig. 1C). There was no apparent difference in the proportion of fluorescent/non-fluorescent oil droplets in different parts of the retina. Oil droplet fluorescence faded within approximately 15 seconds.

When investigating the size of oil droplets, we found that the red/orange oil droplets were the largest, followed by yellow and clear (Table 2, Fig. 2). Oil droplet size varied in different parts of the retina. This pattern was observed in the retinae of all three animals (Turtles 1, 4, and 5) except that in the adult turtle the oil droplets were larger in comparison with those of the juvenile animals (Fig. 2). On average, red/orange oil droplets were found in fewer numbers compared to yellow and clear, ranging from 25% to 29% of the total number of oil droplets. Yellow oil droplet distribution ranged from 32% to 48% and clear oil droplets (both fluorescent and non-fluorescents) ranged from 26% to 40% of the total number of oil droplets.

Focal length and optical sensitivity.—For the calculation of optical sensitivity we measured optical parameters and cone photoreceptor dimensions of turtles of similar sizes (Turtle 2, 3, and 7). In our experiments, both lenses of Turtle 3 showed aberrations, and we found that the focal length varied between 12.0 and 17.0 mm, with a mean focal length of 14.4 mm at a lens diameter of 5.2 mm, resulting in an F number (focal length/lens diameter) of 2.8. The lens of Turtle 7, in contrast, was in good condition (Fig. 3A) and revealed a focal length of 12 mm at a lens diameter of 5 mm and an F number of 2.4.

Our measurements of photoreceptor dimensions (Fig. 3B, Turtle 3) showed that both the diameter and length of cone outer segments varied slightly between the different areas (outer segment diameter: 2.8 ± 0.3 μm [SEM] to 3.0 ± 0.3 μm [SEM]; outer segment length 20.0 ± 3.6 μm [SEM] to 26.6 ± 4.0 μm [SEM]). Outer segments appeared to be shortest in the center of the retina (16.8 ± 3.7 μm [SEM]). Similar results were also observed in Turtle 2.

Using an average cone photoreceptor outer segment length of 20 μm and width of 2.9 μm we calculated the optical sensitivity of the eye of Turtle 3 (Table 3). Sea turtles inhabit shallow waters and the predominant light in their habitat is best described as white light (Lythgoe, 1979). The fraction of white light absorbed by the photoreceptor ($F_{white\ light}$) was calculated as 0.21, which means that almost 80% of the surrounding white light is not absorbed by the photoreceptor. The resulting optical sensitivity (S) was calculated at 0.06 μm^2 sr. With increasing depth in the ocean the downwelling light becomes more and more monochromatic due to scatter and absorption (Jerlov, 1976). Hence, during unusually deep dives Green Turtles might encounter near monochromatic light, which, at the preferred wavelength of the receptor (λ_{max}) would result in a fraction of light absorbed of 0.45 and an optical sensitivity of 0.13.

Ocular media spectral transmission measurements.—Measuring the spectral transmission through the ocular media (cornea, lens, and vitreous humor) of two juvenile Green Turtles (Turtle 5, 6) revealed that the quality of light remains virtually unaltered on its path to the retina (Fig. 4). We found that wavelengths between approximately 350 nm and 700 nm were transmitted equally well, while those below 350 nm were absorbed by the lens and cornea. Wavelength of 50% transmission (T_{50}) for the lens was $T_{50} = 325$ nm and for the cornea $T_{50} = 304$ nm. The vitreous humor transmitted well to below 270 nm. This is below the wavelengths that the Ocean Optics spectrometer is capable of measuring, as a result of which no reliable T_{50} values can be given.

Discussion

Green Turtles (*C. mydas*) are highly visual animals that have well developed retinae containing rods, different types of cones, and oil droplets (Granda and Haden, 1970; Liebman and Granda, 1971, 1975). Granda and Haden (1970) report that oil droplet size varies between different color classes, with orange oil droplets being the largest, followed by yellow and clear. Our study confirms their findings; however, we noticed that the absolute size of oil droplets in

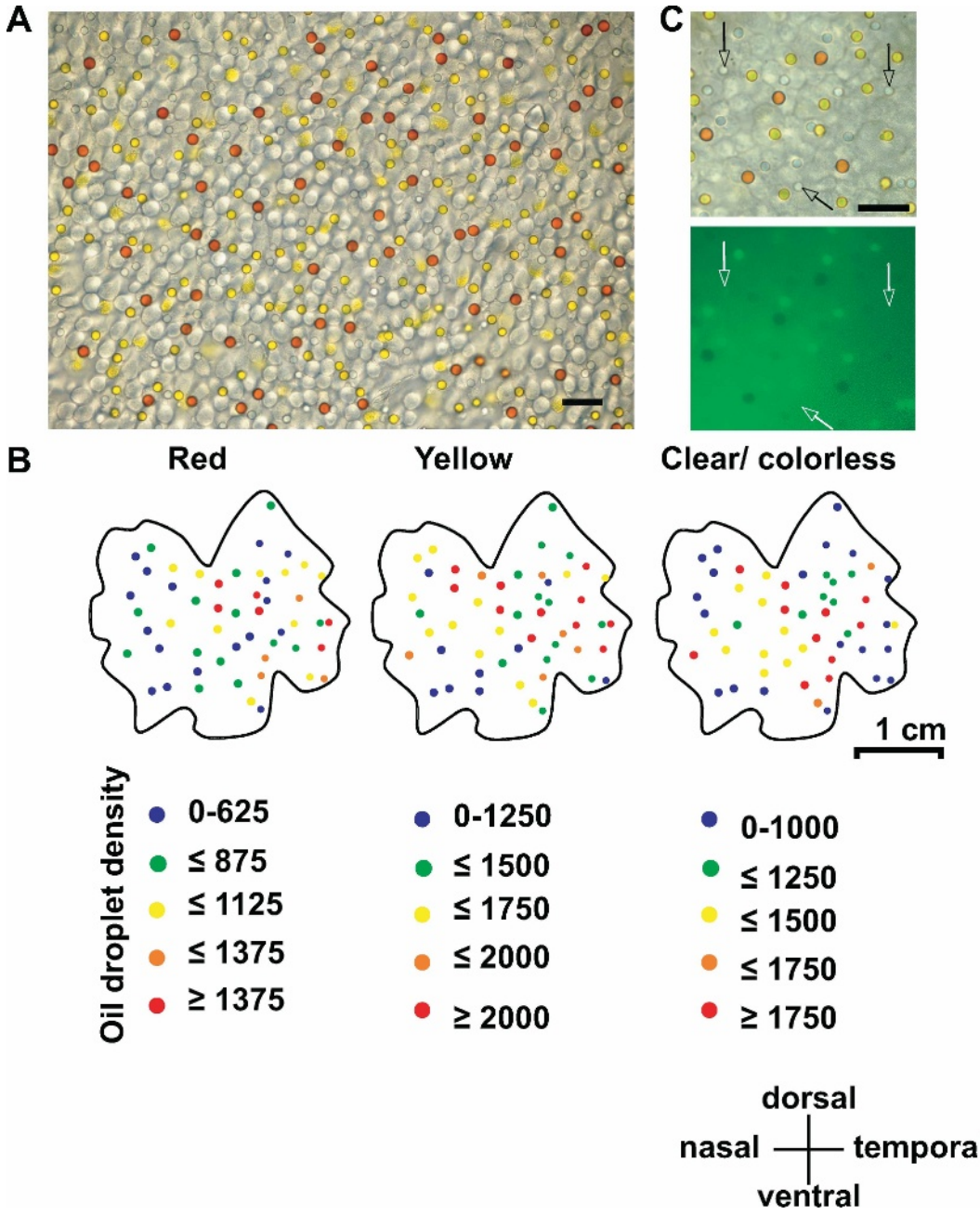

Fig. 1. (A) Image of oil droplets of a whole-mounted Green Turtle retina (brightfield illumination). (B) Topographic map of oil droplet density (number of oil droplets mm^{-2}) in different parts of the retina for red, yellow, and clear oil droplets. Each dot represents one of the areas photographed. Density of all oil droplets (indicated by color) increases towards the central/temporal parts of the retina (data, Turtle 5). Scale bar 25 μm. (C) Two images of the same area of retina under brightfield illumination (top) and ultraviolet (UV) illumination (bottom). These images show that while most oil droplets fluoresce under UV light, a small number do not. Scale bar 25 μm.

TABLE 2. MEAN DIAMETER (IN μM [SEM]; $N = 6$) AND PERCENTAGE DISTRIBUTION (ACROSS AN AREA OF 0.3 MM^2) OF DIFFERENT COLOR CLASSES OF OIL DROPLETS IN FIVE DIFFERENT AREAS OF THE RETINA OF A JUVENILE GREEN TURTLE, *C. mydas* (TURTLE 5).

	Red		Yellow		Clear	
	Diameter	%	Diameter	%	Diameter	%
Dorsal	6.4 (0.09)	26	5.4 (0.04)	48	5.0 (0.08)	26
Temporal	6.3 (0.09)	25	5.0 (0.07)	48	4.6 (0.05)	27
Nasal	5.5 (0.13)	29	4.9 (0.06)	44	4.2 (0.06)	27
Central	5.6 (0.14)	25	4.7 (0.05)	42	4.1 (0.05)	33
Ventral	6.2 (0.06)	28	5.5 (0.09)	32	4.2 (0.05)	40

our study was larger than those found by Granda and Haden (1970). Combining the data from both studies shows that oil droplet size increases with the size of the animal (Fig. 2). Retinal area also increased with the size of the animals, with Granda and Haden (1970) reporting retinal areas of 259 mm^2 in their post-hatchling turtles, while the turtles in our study had retinal areas of 370 mm^2 (Turtle 4, juvenile) and 1270 mm^2 (Turtle 1, adult), respectively. It therefore appears that in Green Turtles, as in many vertebrates, the retina and photoreceptors grow with the body length throughout the life of the animal.

When investigating the distribution of oil droplets we found regional specializations in the Green Turtle retina with the highest densities of all oil droplets found in the central and temporal retina. No such specializations were found by Granda and Haden (1970); however, our study used a slightly different technique that allowed more detailed mapping of oil droplet densities.

Fig. 2. Mean diameters and standard error means (SEM) of oil droplets in Green Turtles of different ages. Data for post-hatchling turtle were taken from Granda (1970), who unfortunately did not specify SEM values. Means for juvenile and adult turtle were taken across the entire retina. There is a significant difference between the diameters of red, yellow, and clear oil droplets of the juvenile and the adult animal (red: $t = 6.21$, $P < 0.01$, $n = 30$; yellow: $t = 2.27$, $P < 0.05$, $n = 30$; clear: $t = 5.24$, $P < 0.01$, $n = 30$).

Similar areal specializations have been found for oil droplets in the freshwater turtle *Pseudemys scripta elegans* (Granda and Haden, 1970) and overall cone densities in the loggerhead turtle *Caretta caretta* (Bartol and Musick, 2001). Interestingly, a visual streak, found to be a dominant feature of the ganglion cell topography of sea turtle (Oliver et al., 2000), is not apparent at the level of oil droplets or cones (Bartol and Musick, 2001; this study). For animals with eyes placed laterally in the head, such as turtles, the temporal retina views the visual field in front. The temporal retina may therefore play an important role in binocular vision. A high number of cones with different oil droplets, and hence different spectral sensitivities, viewing what is in front of the animal is likely to improve discrimination of colorful objects.

Clear oil droplets in the Green Turtle fall into two distinct classes: fluorescent and non-fluorescent, with the fluorescent oil droplet type more dominant (up to 80% of clear oil droplets). In freshwater turtles, fluorescent oil droplets represent two-thirds of the clear oil droplets (Ohtsuka, 1984), although the ratio varies somewhat in the different parts of the retina (Kolb and Jones, 1987). Microspectrophotometry (MSP) studies have shown that the fluorescing oil droplets absorb ultraviolet light and are associated with a different visual pigment than the non-fluorescent oil droplets, which show no significant absorbance at wavelengths greater that 325 nm (Lipetz and MacNichol, 1982; Ohtsuka, 1984, 1985; Loew and Govardovskii, 2001). This type of oil droplet with no selective absorbance is paired with a cone receptor with a spectral sensitivity in the UV waveband (Loew and Govardovskii, 2001). Hence, the presence of a non-fluorescent type of clear oil droplets and our finding of UV transmittance of the Green Turtles' optics suggests visual capabilities in the ultraviolet

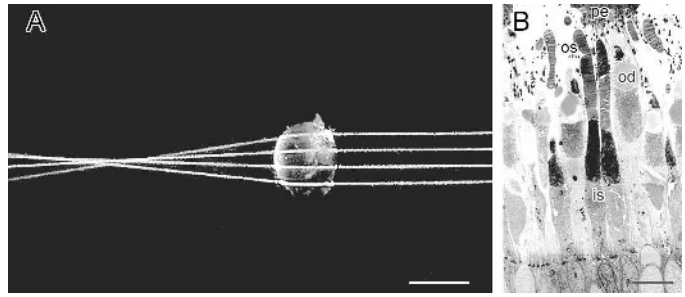

Fig. 3. (A) Example of a composite image obtained from laser ray tracing of a turtle lens (Turtle 7; scale bar, 5 mm). (B) Transmission electron micrograph of cone photoreceptors of Turtle 5 (Scale bar, 10 μm). pe, pigment epithelium; os, outer segment; is, inner segment; od, oil droplet.

waveband at least in the juveniles of this species, as discussed below.

Liebman and Granda's pioneering MSP measurements of the Green Turtle cone photoreceptors revealed three different visual pigments (Liebman and Granda, 1971). They were also able to measure absorbance spectra of yellow and orange oil droplets (Liebman and Granda, 1975). Our study and the comparison with freshwater turtles expand this to suggest that Green Turtles may have four different visual pigments (including a possible UV pigment) and four different oil droplets (red/ orange, yellow, fluorescent clear, and non-fluorescent clear). Liebman and Granda (1975) listed the pairings of the oil droplets and cone photoreceptors measured by them, but the extent to which this was established is unclear (cited in Liebman and Granda, 1971, unpubl. obs.). A number of conflicting studies of oil droplets, such as cone pairings in freshwater turtles (Lipetz and MacNichol, 1982; Ohtsuka, 1985; Loew and Govardovskii, 2001), illustrate how complex these pairings might be in Green Turtles. In fact, for freshwater turtles, *Trachemys scripta elegans*, Loew and Govardovskii (2001) described the pairing, resulting in seven spectrally different cones, as the most complex cone system found in a vertebrate so far. Whether the Green Turtle cone system is approaching this complexity is as yet unknown, and a thorough MSP study is planned to elucidate this.

A possibility for UV vision in Green Turtles.—The spectral sensitivity of a cone photoreceptor is determined by the spectral transmission of the ocular media (cornea, lens, and vitreous humor), the oil droplet and the spectral absorption properties of the visual pigment (Baylor and Hodgkin, 1973; Neumeyer and Jäger, 1985). Spectral transmission measurements through the cornea, lens, and vitreous humor show that UV light to 325 nm is transmitted to the retina, which renders the possibility of UV vision in juvenile Green Turtles, since a prerequisite of UV vision is that UV light is not absorbed at any stage on its path to the retina. During sea finding, newly hatched Green Turtles and loggerhead turtles (*Caretta caretta*) have been shown to respond to light in the UV waveband (Witherington and Bjorndal, 1991). Our results suggest that UV light remains visible to juvenile sea turtles which, like adult Green Turtles, are herbivorous benthic feeders, while hatchling sea turtles are thought to be omnivorous in their pelagic habitat (Mortimer, 1981; Bjorndal, 1997; Hasbún et al., 2000). While the sensitivity to UV light can vary ontogenetically, usually with changes in feeding strategies (Bowmaker, 1990), it seems unlikely that the Green Turtle eye undergoes such changes.

Whether juvenile and adult Green Turtles can perceive UV light will require further microspectrophotometric (MSP) and behavioral studies. Earlier MSP work revealed only three cone visual

TABLE 3. CALCULATION OF OPTICAL SENSITIVITY OF THE EYE OF A GREEN TURTLE AND, FOR COMPARISON, A BLUE TUSKFISH (**Choerodon albigena*, ANATOMICAL DATA FROM ENGSTRÖM, 1963; ALI AND ANCTIL, 1976; AND COLLIN AND PETTIGREW, 1989; SENSITIVITY FROM FRITSCHES ET AL., 2003).

	lens diameter (mm)	focal length (mm)	receptor diameter (μm)	receptor length (μm)	(1) fraction of λ_{max} absorbed	(2) fraction of white light absorbed	sensitivity (μm^2 sr, calculated with (1))	Sensitivity (μm^2 sr, calculated with (2))
C. mydas (Turtle 3)	5.2	14.4	2.9	20	0.45	0.21	0.13	0.06
Blue tuskfish	4.8	6.1	3	15	0.41	0.19	1.4	0.6

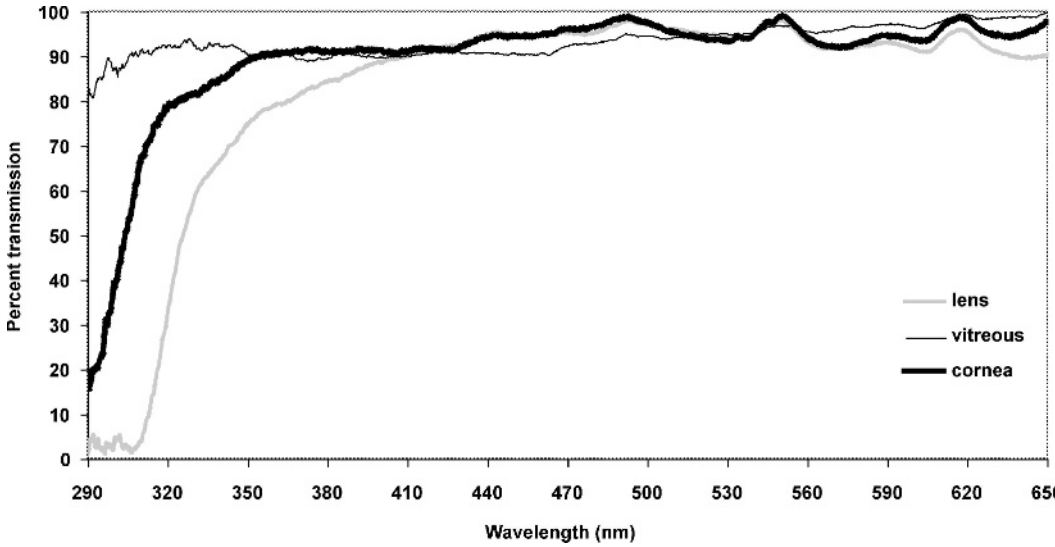

Fig. 4. Spectral transmission measurements of the ocular media (cornea, lens, and vitreous humor) of the Green Turtle. T_{50} values for lens, 325 nm; cornea, 304 nm. No T_{50} value can be given for the vitreous humor since it transmits to wavelengths below the limit of the spectrometer. Data are normalized.

pigments (440 nm, 502 nm, 562 nm; Liebman and Granda, 1975); however, these authors did not appear to test in the UV waveband, most likely due to technical constraints. Ultraviolet radiation is known to be harmful to the retina (Zigman, 1971), and many inhabitants of the tropical marine environment with its high UV radiation and clear water habitats possess UV filters in their ocular media, preventing such potential damage (Fritsches et al., 2000; Siebeck and Marshall, 2000, 2001). The lack of UV filters in the ocular media of sea turtles suggests that UV perception is important in the lives of these animals. Many marine animals, as well as freshwater turtles (*Trachemys dorbignii*; Arnold and Neumeyer, 1987; Ventura et al., 1999) have been reported to have UV vision (e.g., Douglas et al., 1989; Losey et al., 1999). Possible functions for UV vision range from improved foraging ability, species-specific communication of UV body patterns or simply extending the spectral range of an animal's vision (for reviews see Bennett and Cuthill, 1994; Losey et al., 1999). Ultraviolet vision has also been linked to the ability to perceive polarized light (Hawryshyn and McFarland, 1987; Coughlin and Hawryshyn, 1995; Hawryshyn, 2000), which has been suggested to aid many animals in orientation and navigation (Phillips and Waldvogel, 1988; Able and Able, 1993; Rossel, 1993). The possibility that UV vision may function in a similar way in sea turtles is currently under investigation.

Photopic vision is adapted to bright light.—A number of features in the Green Turtle eye suggest that photopic (cone photoreceptor driven) vision is adapted to a bright light environment. A small pupil diameter, long focal length, and the relatively short light gathering sections of the cone photoreceptors (the outer segments) result in a low optical sensitivity of the Green Turtle eye compared to other marine vertebrates and invertebrates (Land, 1981; Fritsches et al., 2003; Collin et al., 2004). The calculation of optical sensitivity has been a useful tool in comparing the light capturing abilities of eyes of very different designs. Optical sensitivities range from extremes such as the exceptionally light sensitive median eyes of the bathypelagic ostracod *Giantocypris* (S = 6100 μm^2 sr) to the foveal daylight vision of humans (S = 0.023 μm^2 sr; Land, 1981), while considering both the optics and the dimensions of the photoreceptors in the eyes studied.

We compared our results for optical sensitivity of the turtle with those of a teleost fish, the Blue Tuskfish (*Choerodon albigena*), which is often found in the same brightly-lit reef habitat as Green Turtles (Table 3; Tuskfish data from Fritsches et al. [2003]). Both Tuskfish and Green Turtles have cone outer segments of similar and relatively small average length and width, resulting in a low fraction of light (*F*) being absorbed by the cones (0.19 and 0.22 for white light and 0.41 and 0.48 for λ_{max} respectively, Fritsches et al. [2003], and this study). The interplay of the

highly varied spectral composition of light underwater at different depths, the reduced absorption of the turtle cones due to oil droplets (Vorobyev, 2003) and the complicated nature of ocular media light absorption in the tuskfish (Siebeck and Marshall, 2000) were not included in the calculation of *F*. However, these different scenarios would result in the value of *F* lying in between those for monochromatic and white light.

The low convergence ratio of cones to ganglion cells (2:1; Bartol and Musick, 2001) is a further indication that the Green Turtle retina is anatomically not equipped for high sensitivity to light (data not available for tuskfish). However, there are a number of neural strategies to improve an animal's sensitivity to light that have not been considered here (Warrant, 1999).

Despite the similarities in photoreceptor dimensions and eye size of Green Turtles and blue tuskfish, we found that the optical sensitivity of Green Turtles was ten times lower (S = 0.13 and 0.06 μm^2 sr for monochromatic and white light, respectively) than the values of blue tuskfish (S = 1.4 and 0.6 μm^2 sr for monochromatic and white light, respectively; Fritsches et al., 2003). This was partially due to the smaller pupil diameters of Green Turtles but mainly caused by the increased focal length in turtles compared to blue tuskfish (Table 3), highlighting a marked difference in eye design of these two aquatic groups of animals.

In fishes, pupil diameters are large, approximating the diameter of the lens (Fernald, 1990) while sea turtles possess small pupils, with diameters at 40–66% of the lens diameter (Northmore and Granda, 1991). It is unknown yet whether sea turtles can change their pupil size with ambient light levels (Northmore and Granda, 1991), but even with a hypothetical maximal pupil dilation approximating the lens diameter the optical sensitivity of sea turtles would only slightly more than double (S = 0.3 and 0.14 μm^2 sr for monochromatic and white light, respectively). Therefore, the main factor reducing optical sensitivity in sea turtles is the longer focal length compared to most fishes.

Similar to fishes, many secondary aquatic vertebrates such as penguins, seals, and sea turtles have spherical or near-spherical lenses. Since the cornea loses all refractive power in water, a spherical lens shape is required in order to concentrate the refractive power of the lens (Sivak, 1988). However, while the hooded seal, for instance, has large spherical lenses and a short focal length that is similar to fishes (Sivak et al., 1989), sea turtles as well as penguins have lenses and pupils that are relatively small compared to the size of the eye, and long focal lengths (Martin and Young, 1984; Northmore and Granda, 1991; this study). The small aperture reduces the light entering the eye and limits resolution. Lengthening the focal length is an optical strategy to increase spatial resolution (Land and Nilsson, 2002) and could be a reason for these animals' long focal length compared to fishes. However, this also drastically decreases the light gathering capabilities of the optics of the turtle eye (Northmore and Granda, 1991; this study). Given the bright light habitat of sea turtles, sensitivity to light, provided by photoreceptor optics, appears therefore not to be a priority for vision in *C. mydas*.

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